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PSYCHE

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ADELPHA (NYMPHALIDAE): DECEPTION ON THE WING*

By Annette Aiello
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Introduction

For the past century, lepidopterists have puzzled over the genus *Adelpha* Hübner, in an attempt to discover the secret character or combination of characters which might lead to a satisfying classification of the 100 or more butterfly species included in this large neotropical group. Several approaches have been tried (Godman & Salvin, 1884, 1901; Fruhstorfer, 1907; Forbes, unpublished manuscript): wing pattern (both upperside and lowerside), wing venation, genitalia, and various combinations of these. If one attempts to coordinate all the information available, the result is a hopeless tangle. As a result, the most obvious set of characters (wing pattern) traditionally has been used in classification; other character groups (genitalia, larvae, pupae) which appear to confuse the situation have been largely ignored. A new strategy is needed, one which would both evaluate the reliability of the different groups of characters already surveyed, and search anew for overlooked sources of information. It was the purpose of my research to review what is known of the immature stages of *Adelpha* species and, based upon that information plus my own observations made in Panama between 1978 and the present, to make speculations regarding species relationships.

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History of Classification

The first attempt at classification within *Adelpha* was made by Godman & Salvin (1884, 1901) with their revision of the 32 species reported from Central America. At that time some 70 species were known for the genus. In their treatment, Godman & Salvin discuss *Adelpha* and its relationship to *Limenitis* and note that several species *(bredowi, populi, camilla, lorquini)* are difficult to assign to either genus. Distribution of such characters as eye pubescence, venational differences, variation in proportions of male leg segments, and peculiarities of male genitalia within *Adelpha-Limenitis* is surveyed. Classification of the 32 species begins with isolation of *A. bredowi* (eyes smooth in front) from all others (eyes hairy in front) and continues by arranging the other 31 species using gross features of wing pattern. The result is eleven groups, six of which are represented by single species.

With Fruhstorfer (1907) came the first and only published revision of the entire genus *Adelpha.* The 90 species treated are assigned to two main groups based upon the length of the forewing discal cell; short = *Adelpha* group, elongate = *Heterochroa* group. Upon this division, Fruhstorfer comments, "Anatomically there are also two series [male genitalia with or without clunicula] of species distinguishable. They, however, do not agree with those based upon the structure [discal cell length]." The linear arrangement of species within the largest group (*Heterochroa* with 82 species) reflects presumed relationships based upon wing pattern features.

Fruhstorfer touches upon but does not pursue the possibility of a closer than realized alliance between New and Old World groups. In his introduction he notes that the male clasping organs of *Adelpha* "...approach those of the [Old World] genus *Pantoporia (Athyma)* in such a way that...it would be quite impossible to ascertain where organs or photes [sic] of them belong to, which are not denominated." Concerning the male valves, he further observes, "...there exist also nearly square ones with 2 or 3 small acicular teeth (resembling a *Limenitis [Moduza] procris* from India and Ceylon)."

Fruhstorfer's revision included a number of misidentifications, which presumably were corrected by Hall (1938) following examination of the original material.

At the time of his death (1968) W. T. M. Forbes had made a good deal of progress on a revision of *Adelpha,* and his manuscript is in

the Archives of the Museum of Comparative Zoology, Harvard University. About half of this manuscript is in a nearly illegible hand; half is typewritten. The typed portion includes part of an introduction, notes on each species, a key (based upon wing pattern) to species and species groups, and descriptions of four new species. Included also are more than 70 genitalic illustrations (inside of right valve) by Howarth. Forbes had analyzed these latter and was in the process of constructing a key to genitalia. His two approaches, of wing pattern and genitalia, yielded different species groupings, and it is not clear whether he favored one of these, or intended to use a combination of the two in his final classification.

Of the immature stages of *Adelpha,* very little has been said, and what has been said has been largely ignored for the simple reason that this new information appears to confuse matters rather than clarify them.[1] Forbes (uncompleted manuscript) had read Moss's (1933) paper on *Adelpha* larvae and pupae, and had examined several pupal skins of *Adelpha* and Old World Limenitini in the collections of the British Museum (Natural History) when he commented, "The larvae and pupae are highly varied and unless a high percent are misdetermined, show characters wholly incongruent with adult structures and patterns."

The fact that, within *Adelpha,* the study of adult characters results in species-alignments different from those obtained by consideration of the immature stages and/or genitalia, suggests that at least one set of characters is unreliable or perhaps even deliberately deceptive.

Immature Stages

Due to taxonomic confusion within *Adelpha,* it is impossible to know how many species actually are represented by the 34 or so life history accounts published for this genus. My estimate is that at least 24 species are illustrated (including illustrations in this paper) as final instar larva, or pupa, or both, many of these by more than one author. Most accounts, whether illustrated or not, include a foodplant record.

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[1]This author has located only four publications (Moss, 1933; Müller, 1886; Young, 1974; Comstock & Vasquez, 1960) which figure any immature stages of *Adelpha;* several publications present descriptions only.

In the present paper, all illustrated reports are reviewed to see whether it is possible to distinguish natural species groups within the genus *Adelpha.*

Oviposition

Judging from the few scattered reports (Table 1) of oviposition in the Limenitidini, eggs are laid singly and are usually placed at the tips of leaves. While many accounts do not specify whether placement is on the upper or lower surface, the majority that do specify, report upper surface oviposition.

Adelpha iphicla females alight upon a leaf and walk backwards while searching for the desired oviposition site with the tip of the abdomen; the egg is then placed and the butterfly takes flight before her next oviposition, which may be on the same leaf. In the case of lower surface oviposition, the female merely bends her abdomen around the edge of the leaf and touches its tip to the leaf.

Among the six species of *Adelpha* whose eggs were collected in Panama, four (Table 1) place their eggs along damaged portions of leaves, especially on jagged points, as well as at the leaf tip, and one of these *(A. iphicla)* is about as likely to lay eggs along an intact leaf margin as at the tip. As well, a female *A. iphicla* may return to the same leaf several times and place as many as four eggs on one leaf, often on its undersurface.

Eggs

Eggs of the seven *Adelpha* species (*basiloides, cocala, cytherea, marcia, iphicla, melanthe, phylaca aethalia,* and *salmoneus*) examined by this author, were all similarly sculptured (figure 1) with pits (hexagonal due to packing) and seta-like projections (one from each junction of three pits). This same sculpture type is figured for *Limenitis* by both [2]Scudder (1889) and Eltringham (1923).

Young's (1974) description of the egg of *Adelpha leucophthalma* as having the seta-like projections "aris[ing] from the facets," is doubtful.

Also doubtful is the account by Comstock and Vazquez (1960) which describes and illustrates the egg of *A. celerio* as having convex rather then concave hexagons. Such an error is easily made, as these

[2]As *Basilarchia.*

Table 1. Placement of egg on leaf by various members of the Limenitidini (Nymphalidae)

BUTTERFLY SPECIES	EGG PLACEMENT	REFERENCE
Adelpha basiloides Bates	T↓, D↓	Aiello
Adelpha celerio diademata Fruh.	T	Comstock & Vazquez (1960, pg. 407)
Adelpha cocala Cr.	T↓, (D↓)	Aiello
Adelpha cytherea (?)	↑	Müller (1886, pg. 484)
Adelpha iphicla L.	T↓(↑), M↓(↑)	Aiello
Adelpha iphicla	↑	Müller (1886, pg. 484)
Adelpha isis Dru.	T↓, D↓	Müller (1886, pg. 481)
Adelpha leucophthalma tegeata Fruh.	D↓	Young (1974, fig. 2)
Adelpha melanthe Bates	D↓	Aiello
Adelpha phylaca aethalia Feld.	T↓	Aiello
Adelpha plesaure	T↓	Müller (1886, pg. 484)
Adelpha salmoneus Butl.	T↓, (D↓)	Aiello
Adelpha serpa	T↓	Müller (1886, pg. 484)
Adelpha syma Godt.	T	Hoffmann (1937, pg. 212)
Athyma nefte Cr. (as *Parathyma nefte* Cr.)	T↓, (M↑)	Morrell (1954, pg. 160)
Athyma opalina Kollar	↑	Robson (1894, pg. 338)
Lasippa tiga Moore (as *Neptis heliodore* Fruh.)	T	Morrell (1954, pg. 160)
Limenitis archippus (as *Basilarchia archippus)*	T↑	Scudder (1889, fig. 16)
Limenitis lorquini burrisonii Maynard	T	Dornfeld (1980, pg. 61)
Moduza procris Cr.	T	Morrell (1954, pg. 157)
Neptis nata Moore	T	Morrell (1954, pg. 162)

T = leaf tip (tooth, in case of *A syma*), M = leaf margin (intact), D = damaged portion of leaf, ↓ = upper surface of leaf, ↑ = lower surface of leaf, ( ) = less commonly

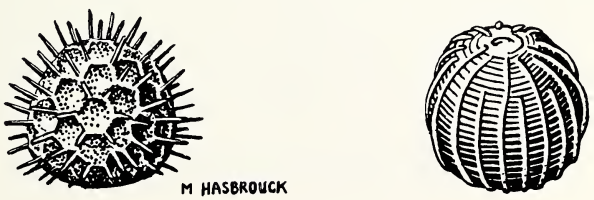

Figure 1. Eggs of *Adelpha* (left) and *Doxocopa* (right).

eggs can present an optical illusion, however, an edge view of a partly eaten egg shell shows clearly that the hexagons are indeed pits.

Comstock and Vazquez (1960) also describe and figure a differently sculptured egg, which they call *A. iphicla* with the reservation that it might actually be an egg of [3]*Doxocopa.* Because their larvae died soon after hatching, the authors never knew that they had indeed been fooled by the ovipositing *Doxocopa* female, a mimic of *Adelpha.* My own rearing of *Doxocopa laure* (LOT 83-6) was from two eggs with pattern (figure 1) identical to that in figure 33 of their paper. My reared *Adelpha iphicla* were from eggs patterned as those of all the other *Adelpha* species examined so far. Possibly this egg sculpture pattern will be found throughout the Limenitini and may prove useful in defining tribal limits.

Development Time

Oviposition was observed only for *Adelpha iphicla,* and each of the three fresh eggs collected required 5 days development before the first instars emerged. Of five other species collected as eggs, of unknown age, three had longer minimum egg-development times than did *A. iphicla: A. basiloides* (LOT 82-65), one egg hatched after 6 days; *A. cytherea* (LOT 83-3), one egg hatched after 7 days; and *A. salmoneus* (LOT 83-14), two eggs hatched after 6 days.

Because individuals were collected at various stages of development, total time from hatching to eclosion could be determined for only a few individuals of ten species. In spite of the fact that the resulting data (Table 2) is not uniform, it is clear that development time is variable, and often more so within a species than between species. The extreme example of wide variation is in *A. basiloides* which has a longer development time than other species, and which sometimes passes through six instars instead of the usual five. Five 6-instar individuals of *A. basiloides* were encountered, and these were from four separate rearing lots, each of which included 5-instar individuals as well. Each of these lots was collected on *Amaioua corymbosa;* larvae collected on *Alibertia edulis* and *Bertiera guianensis* did not produce extra instars. In spite of the additional instar, 6-instar individuals did not require longer development times

[3]As *Chlorripe.*

than 5-instar individuals, however, larvae on *Amaioua,* regardless of number of instars, were slower to develop (41–48 days) than were larvae on *Alibertia* or *Bertiera* (32–44 days).

Larvae

Miles Moss reared twelve species of *Adelpha* from Pará, Brasil, and illustrated (1933) the final instar larva and the pupa for each of them. In spite of the lack of detail in his illustrations and descriptions, and the fact that his scheme for numbering body segments omits abdominal segment-9, his little paper remains the masterpiece on *Adelpha* immatures. It was Moss who realized (page 15) that:

> "...systematists,...by a careful examination of certain hitherto unsuspected points of likeness or dissimilarity between the species in their early stages, may perhaps be led to modify the existing order and grouping of the butterflies of this difficult genus. It is just possible that a few unexpectedly close relationships may thus be established, while others at present confused, or regarded as near of kin, may be found to be more distantly related than was supposed."

He concluded that *A. cytherea,* and *pseudococala* are closely related, also *delphicola* and *mesentina,* and *serpa* and *paraëna*. My analysis of published illustrations and live material lends support to Moss's groupings and adds several more.

First instar larvae

First instar larvae, of all species which I have seen, appear identical in form, and are some shade of brown or grey. The head bears setae, but none of the ^{4}chalazae of later instars; pale bumps on the body are found where the future ^{4}scoli will be, and the body is covered with tiny pale spots each centered with a minute seta. After their first meal, larvae take on the green color of their foodplant, although the head remains brown.

Second instar larvae

From the second instar on, the head is ornamented with chalazae which give it a spiny appearance. The face has numerous round,

Table 2. Duration (in days) of larval instars and pupal stage for twelve *Adelpha* species.

Species	Instar 1	2	3	4	5	6	Pupa	Total Time 1–Adult
basiloides (5-instar)	4–7 [10]	3–8 [15]	3–6 [17]	4–10 [21]	6–14 [18]	–	8–11 [20]	39–48 [9]
basiloides (6-instar)	m6 [1]	6–7 [4]	4–7 [5]	3–(4) [5]	3–6 [5]	7–11 [5]	8–11 [5]	48 [1]
celerio	–	–	m3 [1]	8 [1]	11 [1]	–	10 [1]	–
cocala	4, 5 [2]	3–5 [4]	4–5 [5]	4–(6) [8]	7–13 [7]	– –	8–11 [7]	35, 39 [2]
cytherea	4 [1]	3, 4 [2]	3, 4 [2]	(3), 10 [3]	(6)–10 [4]	– –	7, (9) [4]	28 [1]
iphicla	(4), 7 [4]	(3)–7 [11]	(3)–6 [23]	1–7 [24]	4–10 [32]	– –	7–10 [27]	29 [3]
isis (in Müller, 1886)	5 [1]	6 [1]	4 [1]	5 [1]	9 [1]	– –	13 [1]	42 [1]
justina	m4 [2]	4 [2]	3, 4 [3]	3, 4 [3]	4–6 [3]	– –	6–9 [4]	m30 [1]

Table 2. (Continued) Duration (in days) of larval instars and pupal stage for twelve *Adelpha* species.

Species	Instar 1	2	3	4	5	6	Pupa	Total Time 1-Adult
leucophthalma	–	6 [1]	4 [3]	4, 5 [3]	6–(7) [4]	–	9 [3]	–
melanthe	m5 [1]	m4 [2]	4 [1]	4 [1]	10 [1]	–	10 [1]	m37 [1]
nr. *paraëna*	–	–	–	7 [2]	12, 13 [2]	–	10 [2]	
phylaca aethalia	m4 [1]	m4 [2]	3, 7 [2]	6, (7) [6]	7–9 [8]	–	8–11 [7]	m41 [1]
salmoneus	(4), 5 [3]	3–5 [4]	4–6 [5]	3–(5) [6]	6–12 [6]	–	9, 10 [4]	32, 35 [2]

Unless otherwise noted, the above data was collected in Panamá by the author.
[ ] = n
( ) = commonest number of days in cases of strong bias towards one end of range; otherwise, ranges are normal curves.
m = minimum number of days in cases where full time for an instar is not known.

flatbottomed pits which first appear in small numbers in instar two, three, or four depending upon the species. These may be the same color as the rest of the head capsule or may be a contrasting color. Facial stripes appear in the fourth instar of some species as well.

The body now bears stubby scoli (each with 3–5 radiating apical spines). These scoli are arranged in three rows (subdorsal, supraspiracular, and subspiracular), thus, each body segment has three pairs of scoli. The subdorsal scoli on thoracic segments 2 & 3 and abdominal segments 2, 7, & 8 are very slightly larger than the others, but all are similar in form.

Beginning with the second instar there are color and pattern changes in some species, but most are fairly uniformly colored (brown, green, or black) and have paler scoli and tiny spots, much as the first instar. In *Adelpha basiloides,* the larval color depends upon the foodplant; larvae are light brown or reddish brown on *Amaioua,* and dark brown on *Alibertia* and *Bertiera.*

THIRD AND FOURTH INSTAR LARVAE

From instar three on, the face is framed by two distinct rings of chalazae, and body scoli show further development, especially those scoli which will be the largest or most distinctive in the final instar. By late fourth instar, body scoli have become swollen at the bases due to developing final instar scoli inside. In these two instars, the scolus spines are pale, and as before, the body is speckled with tiny pale spots.

A dorsal, paler patch ("saddle") appears in the third or fourth instar of many species. In *A. salmoneus* and *cytherea* the "saddle" is faint and extends from abdominal segment 2 or 3 through segment 6. *A. cocala* and *leucophthalma* may have a "saddle" on abdominal segments 5–6. *A. justina* is pale dorsally from thoracic segment 2 through abdominal segment 8. *A. basiloides,* nr. *paraëna,* and *celerio* have a triangular "saddle" with its base on the posterior portion of abdominal segment 4, and its apex at mid abdominal segment 6. In the latter two species the "saddle" is poorly defined; in *A. basiloides* it is sharply demarcated.

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[4]Terminology of Peterson (1962). CHALAZAE(AE): a distinctly elevated cone-shaped area, bearing 1–3 simple setae; (SCOLUS(I): an elongated projection, bearing 4 or more setae or spines.

FINAL INSTAR LARVAE

Final instar larvae (Figures 4 & 5) of all species studied have several things in common. The head (Figure 2) has a spiny appearance owing to the numerous chalazae which frame the face. These seem to be fairly constant in number and position (Figure 3) and to vary from species to species mainly in their relative size. *A. iphicla* for example has a relatively smooth face because it lacks several of the chalazae found in other species. *A. phylaca* and especially *melanthe* are the spiniest in appearance due to numerous additional setae. Color and pattern also vary: *A. celerio* has a striped face, *A. basiloides* and *A. cocala* patterned ones. The pits of *A. cytherea* are darker than the rest of the face; the head of *A. salmoneus* is reddish and constrasts strongly with its green body.

Each body segment bears three pairs of scoli (subdorsal, supraspiracular, and subspiracular); there are no dorsal scoli. While the scoli are variable in form and length, in all species studied, those of the prothorax and abdomen-1 are either very short or are reduced to a few spines. Usually the longest are the subdorsal scoli of meso- and meta-thorax and abdomen-2, -7 & -8, and the supraspiracular scoli of the meso-thorax. In many species the subdorsal scoli of abdomen-2 are the most distinctive in form and often are curved backwards.

Body scoli are diverse but the various forms can be grouped into two main types: those which are terete (round in cross-section), and those which are flattened.

The terete scolus, in its simplest form, is a short stalk with 3–5 spines radiating star-like from its apex (e.g., [5]scoli A3–6 of *A. celerio, cytherea, salmoneus,* and *justina*). More complex scoli are slender and longer with spines at intervals along their full length, and either with one to a few ascending spines towards the apex (thoracic scoli of many species, e.g., *A. phylaca, melanthe, cocala, basiloides, cytherea, justina, salmoneus*), or with 3–5 radiating apical spines (e.g., scoli of A3–6 in *A. phylaca, melanthe*). Scoli also may be short and thick with a dense covering of spines (e.g., A2 of *A. cocala, leucophthalma, basiloides*), or be club-shaped and more sparsely spined (e.g., A8 of *basiloides*).

[5]Throughout the remainder of this paper, "scolus(i)" refers to the subdorsal set unless otherwise noted; T = thorax, thoracic segment; A = abdomen, abdominal segment.

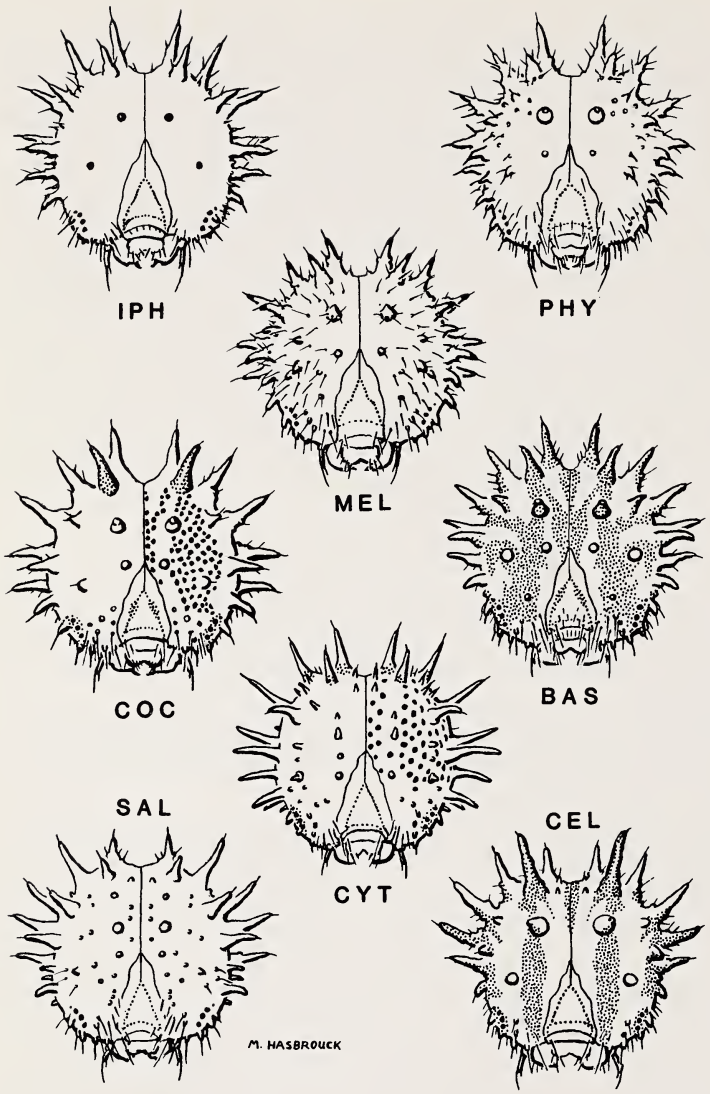

Figure 2. Faces of final instar larvae of *Adelpha* species reared in Panamá: BAS = *basiloides*, CEL = *celerio*, COC = *cocala*, CYT = *cytherea marcia*, IPH = *iphicla*, MEL = *melanthe*, PHY = *phylaca aethalia*, SAL = *salmoneus*.

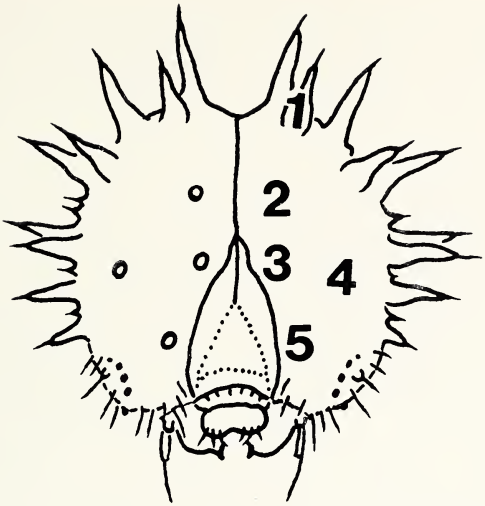

Figure 3. Location of head chalazae 1–5, referred to in text.

Flattened scoli have a plumose or leaf-like appearance (e.g., *A. celerio, serpa, paraëna*) which is due not only to the arrangement of spines in two opposite rows along the scolus, but also to the flattening and widening of those spines which may take on spatulate, elliptical, or lanceolate forms, and may be so crowded that they overlap one another. In the case of extremely condensed scoli, the spines appear to fuse with one another (see *A. serpa* in Müller, 1886).

Larval Behavior

Upon hatching, a larva eats some or all of its egg shell and then feeds on the leaf tip leaving the midrib intact. Larvae rest out on the midribs which they have exposed, and eventually extend them by addition of fecal pellets held in place with silk. Most larvae fashion several such supports during each instar, often using lateral veins instead of the midrib. When not feeding, *Adelpha* larvae rest out on their supports, facing away from the leaf; molting takes place on the support as well. After they molt to the final instar, larvae abandon their supports and thereafter rest on the upper surface of a leaf.

In addition to the above behavior, typical of many nymphalid butterfly species, first through fourth instar *Adelpha* larvae engage in an odd practice not known for other New World butterflies; they accumulate their fecal pellets, fastening them in place with silk, to form a mass which either surrounds the base of the support or is suspended beneath it. This mass may include bits of leaf in *A. iphicla,* or consist of more leaf than feces in *A. phylaca* and *melanthe.* The work of *A. basiloides* is the most distinctive because, in addition to the mass just described, this species consistently constructs a small, usually curved, larva-form mass on the leaf surface, several mm away from either the leaf edge or the usual mass. Upon viewing this artistry, one cannot help imagining that it serves as a decoy larva to discourage would-be predators. A single reared individual of *A. iphicla* also engaged in this behavior, but excepting that, I have observed it only in *A. basiloides.*

Resting larvae position their bodies in one of several ways:

(1) Straight Position (figures 4 & 5). Larvae in any instar may use this position, and typically when out on their supports they rest this way.

(2) Front-Curved Position, as shown in Young (1974, fig. 2. B, C). In this position, the larva grasps its support with the prolegs only, and raises and curves its anterior portion (head through A2) so that the head is somewhat inclined, and the toracic scoli are directed forwards. Larvae about to molt use this position; the second instar in Young's (1974, fig. 2C) photograph has a swollen pro-thorax and is probably preparing to molt to third instar. Final instar larvae of *A. justina* use a raised but uncurved version of this position instead of the usual final instar stance, described next.

(3) Front-Arched-Rear-Up Position. This position is typical of final instar larvae but occurs in earlier instars as well. Involved are the raising and arching of the anterior portion of the body (head through A2), plus elevation of the posterior portion (A7–10). In addition, the thoracic scoli are directed forwards, and those of A2 are held backwards. In this position, the face and the area at the top of the arch (T3 through A2) are parallel to each other and to the substrate. This and the next position are assumed when the larva is disturbed.

(4) Curled Position. The larva curls to one side into a "C" or "J" shape on the upper surface of the leaf; the rear portion (A7–10) may or may not be elevated. *A. celerio* often rests in this position,

and when it does, the scoli on the outside of the curve stick out all around and the animal resembles a bit of moss. Moss (1933) reported the same behavior and appearance for *A. thesprotia.*

Foodplants

At first inspection, it would appear that larvae of *Adelpha* butterflies are not very particular about their foodplant selection. Indeed, some 56 plant species, representing 42 genera and 16 families have been reported as larval foodplants of *Adelpha.* Moreover, many *Adelpha* species are known to be polyphagous: *A. melanthe, delphicola,* and *isis* have each been reared on three plant genera, *A. celerio* on four, and *A. cocala* and *iphicla* each on eight. *Cecropia* (Cecropiaceae), *Sabicea* (Rubiaceae), and *Vitex* (Verbenaceae) are each attacked by five different species of *Adelpha.*

However, when larval foodplants are grouped by the butterfly species which feed upon them (Table 3), a pattern does emerge: *Adelpha* species fall nicely into two main feeding groups: (1) Rubiaceous feeders, and (2) Non-rubiaceous feeders.

With the following three exceptions, butterfly species that feed upon members of the Rubiaceae have not been reported on plants outside that family. *A. boreas tizona* was reared on both Rubiaceae and Ericaceae (Marquis and DeVries, unpublished); *A. cocala,* reared on seven members of the Rubiaceae, also has been reported on *Emmotum* of the Icacinaceae (Moss, 1933); *A. syma,* on Rubiaceae and Rosaceae. The record of *A. iphicla iphicleola* on *Celtis* (Ulmaceae) (Comstock and Vazquez, 1960) is in error; their butterfly was actually *Doxocopa,* misidentified as *Adelpha.*

It is interesting to note that the rubiaceous genera, utilized as foodplants by *Adelpha,* belong to at least seven of the 18 tribes outlined for the Rubiaceae by Kirkbride (1982).

Several non-rubiaceous feeders do show wide foodplant preferences, the extreme examples being: *A. melanthe* which feeds on three plant genera representing three families, and *A. celerio* which feeds on five genera in four families. The only common bond among the foodplants of these two butterflies seems to be that all are scabrous- or pubescent-leaved, second-growth trees. Some plants attract a more specialized group of feeders: *Vitex* (Verbenaceae) is attacked by *A. abia, calliphane, epizygis,* and *jordani,* which have not been reported on any other plants. *A. naxia ipiphilca,* also

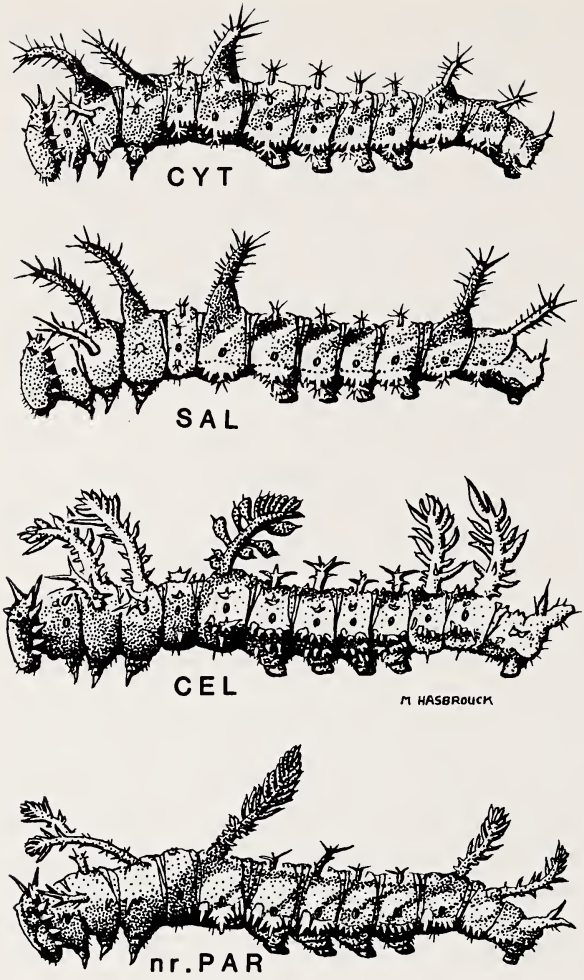

Figure 4. Final instar larvae of *Adelpha* species reared in Panamá: abbreviations are the same as in Figure 2 except that CEL = nr. CEL; in addition nr. PAR = near *paraëna*.

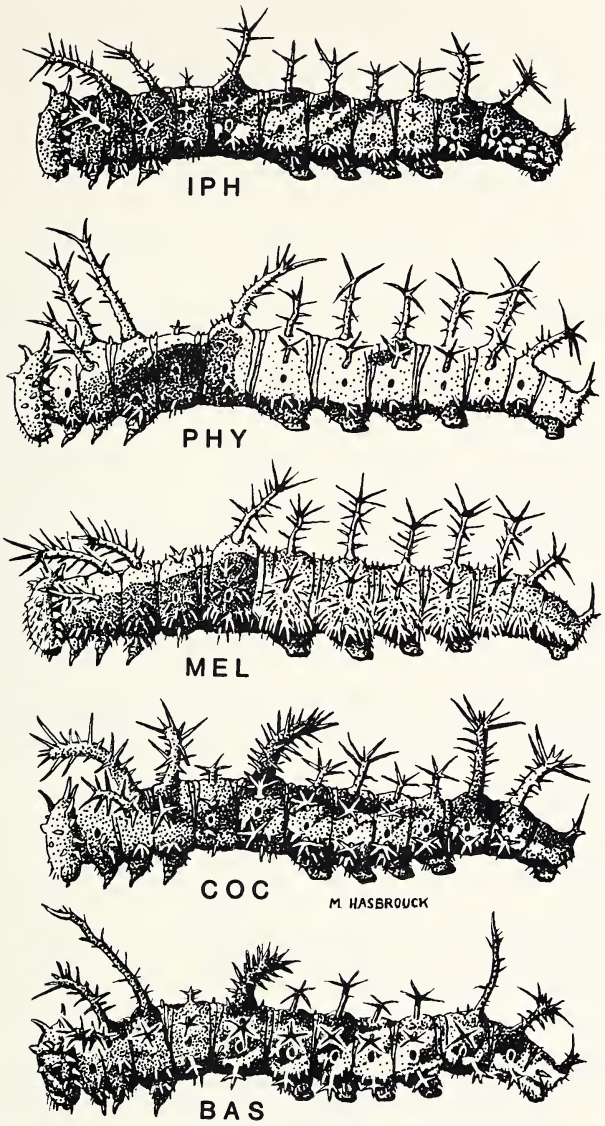

Figure 4. (Continued)

Table 3. Larval foodplants reported for *Adelpha* species, arranged alphabetically by butterfly species.

Adelpha species/ foodplant	Plant Family	Locality	Reference
ABIA			
Vitex sp.	Verbenaceae	Brasil	Müller (1886)
BASILEA			
Calycophyllum sp.	Rubiaceae	Cuba	Dewitz (1879)
BASILOIDES			
Alibertia edulis	Rubiaceae	Panamá	Aiello LOTS 79-121, 80-38, 81-17, 81-42, 81-49, 83-16, 83-42
Amaioua corymbosa	Rubiaceae	Panamá	Aiello LOTS 82-59, 82-65, 82-70, 82-72, 83-42
Bertiera guianensis	Rubiaceae	Panamá	Aiello LOTS 82-64, 82-73, 83-87
Ixora nicaraguensis	Rubiaceae	Panamá	Mallet in DeVries (unpub)
BOETIA OBERTHURI			
Luehea seemannii	Tiliaceae	Costa Rica	Mallet in DeVries (unpub)
BOREAS TIZONA			
Satyria sp.	Ericaceae	Costa Rica	Marquis in DeVries (unpub)
Chomelia bispinosa	Rubiaceae	Costa Rica	DeVries (unpub)
BREDOWI CALIFORNICA			
Quercus chrysolepis	Fagaceae	California	Orsak (1977)
Quercus spp. (especially *chrysolepis*	Fagaceae	California	Howe (1975)
Quercus spp.	Fagaceae	California	Dornfeld (1980)
BREDOWI EULALIA			
Quercus spp.	Fagaceae	Mexico, US	Ferris & Brown (1980)
CALLIPHANE			
Vitex montevidensis	Verbenaceae	Brasil	cited in Lima (1968)
CALLIPHICLEA			
Ilex paraguariensis	Aquifoliaceae	Paraguay	Jorgensen (1921)
CELERIO			
Cecropia peltata	Cecropiaceae	Panamá	Coley LOT 15
Miconia argentea	Melasto-mataceae	Costa Rica	Mallet in DeVries (unpub)
Ochroma pyramidale	Bombacaceae	Panamá	Aiello LOT 82-41
Ochroma pyramidale	Bombacaceae	Panamá	Coley LOT 22
Urera sp.	Urticaceae	Costa Rica	DeVries (unpub)

Table 3. (continued)

Adelpha species/ foodplant	Plant Family	Locality	Reference
CELERIO DIADEMATA			
Conostegia xalapensis	Melasto-mataceae	Mexico	Comstock & Vazquez (1960)
Miconia sp.	Melasto-mataceae	Mexico	Comstock & Vazquez (1960)
nr. CELERIO			
Heliocarpus popayanensis	Tiliaceae	Panamá	Aiello LOTS 82-75, 83-68
COCALA			
Calycophyllum candidissimum	Rubiaceae	Panamá	Aiello LOT 81-44
Calycophyllum candidissimum	Rubiaceae	Costa Rica	Janzen 81-SRNP-740 in DeVries (unpub)
Chomelia psilocarpa	Rubiaceae	Panamá	Aiello LOT 81-14
Emmotum nitens?	Icacinaceae	Brasil	Moss (1933)
Malanea sp.	Rubiaceae	Brasil	Moss (1933)
Pentagonia macrophylla	Rubiaceae	Costa Rica	DeVries (unpub)
Psychotria sp.	Rubiaceae	Costa Rica	Marquis in DeVries (unpub)
Uncaria tomentosa	Rubiaceae	Panamá	Aiello LOT 81-54
Warscewiczia coccinea	Rubiaceae	Panamá	Aiello LOT 82-66, 82-71, 82-74
CRETON			
Quercus?	Fagaceae	Mexico	Miller & Miller (1970)
CYTHEREA			
Sabicea aspera	Rubiaceae	Brasil	Moss (1933)
CYTHEREA MARCIA			
Sabicea panamensis	Rubiaceae	Panamá	Aiello LOT 83-129
Sabicea villosa	Rubiaceae	Panamá	Aiello LOTS 82-26 83-3
Sabicea villosa	Rubiaceae	Costa Rica	DeVries (unpub)
DELPHICOLA			
Bombax munguba	Bombacaceae	Brasil	Moss (1933)
Cecropia sp.	Cecropiaceae	Brasil	Moss (1933)
Pourouma sp.	Cecropiaceae	Brasil	Moss (1933)
DEMIALBA			
Rondeletia sp.	Rubiaceae	Costa Rica	Haber in DeVries (unpub)
DONYSA			
Quercus?	Fagaceae	Mexico	Miller & Miller (1970)

Table 3. (continued)

Adelpha species/ foodplant	Plant Family	Locality	Reference
EPIZYGIS			
Vitex montevidensis	Verbenaceae	Brasil	cited in Lima (1968)
EROTIA			
Tetrapteris sp.	Malpighi-aceae	Brasil	Müller (1886)
FESSONIA			
Randia echinocarpa	Rubiaceae	Costa Rica	Janzen 79-SRNP-216 in DeVries (unpub)
Randia learstenii	Rubiaceae	Costa Rica	Janzen 79-SRNP-725 in DeVries (unpub)
IPHICLA			
Antirrhoea trichantha	Rubiaceae	Panamá	Aiello LOTS 81-25, 82-27, 83-41
Alseis blackiana	Rubiaceae	Panamá	Aiello LOTS 82-36, 82-56, 82-63, 82-69
Bathysa sp. nr. *barbinervis*	Rubiaceae	Brasil	Müller (1886)
Calycophyllum candidissimum	Rubiaceae	Panamá	Aiello LOTS 81-34, 81-78
Calycophyllum candidissimum	Rubiaceae	Cuba	Riley (1975)
Gonzalea spicata	Rubiaceae	W.I.	Barcant (1970)
Gonzalea spicata	Rubiaceae	W.I.	Riley (1975)
Isertia haenkeana	Rubiaceae	Panamá	Aiello LOT 81-16
Rondeletia panamensis	Rubiaceae	Panamá	Aiello LOTS 83-101, 83-111
Uncaria (as *Ourouparia*) *guianensis*	Rubiaceae	Brasil	Moss (1933)
Uncaria tomentosa	Rubiaceae	Panamá	Aiello LOTS 81-46, 81-51
IPHICLA EPHESA (as *ephicla ephesa*)			
Bathysa sp.	Rubiaceae	Brasil	cited in Lima (1968)
IPHICLA IPHICLEOLA			
Calycophyllum candidissimum	Rubiaceae	Costa Rica	Janzen 79-SRNP-135 in DeVries (unpub)
IPHICLA IPHICLEOLA (*Doxocopa* misidentified as *Adelpha*)			
Celtis sp.	Ulmaceae	Mexico	Comstock & Vazquez (1960)

Table 3. (continued)

Adelpha species/ foodplant	Plant Family	Locality	Reference
ISIS			
Cecropia pachystachia	Cecropiaceae	Brasil	cited in Lima (1968)
Cecropia pachystachia	Cecropiaceae	Brasil	Müller (1886)
Coussapoa schottii	Cecropiaceae	Brasil	cited in Lima (1968)
Coussapoa schottii	Cecropiaceae	Brasil	Müller (1886)
Pourouma acutiflora	Cecropiaceae	Brasil	cited in Lima (1968)
Pourouma acutiflora	Cecropiaceae	Brasil	Müller (1886)
JORDANI			
Vitex triflora	Verbenaceae	Brasil	Moss (1933)
JUSTINA JUSTINA			
Alternate-leaved plant	?	Panamá	Aiello 83-23, 83-67
LARA	Cecropiaceae	Trinidad	M. J. W. Cock (pers. comm.)
LEUCOPHTHALMA			
Pentagonia wendlandia	Rubiaceae	Costa Rica	Young (1974)
Undetermined	Rubiaceae	Panamá	Aiello LOTS 83-22, 83-24, 83-25
Undetermined	Rubiaceae	Costa Rica	DeVries (unpub)
MELANTHE			
Cecropia sp.	Cecropiaceae	Costa Rica	DeVries (unpub)
Trema micrantha	Ulmaceae	Panamá	Aiello LOT 83-8
Trema micrantha	Ulmaceae	Costa Rica	DeVries (unpub)
Urera sp.	Urticaceae	Costa Rica	DeVries (unpub)
MELONA			
Malanea sp.	Rubiaceae	Brasil	Moss (1933)
MESENTINA			
Pourouma sp.	Cecropiaceae	Brasil	Moss (1933)
MYTHRA			
Bathysa sp. nr. *barbinervis*	Rubiaceae	Brasil	Müller (1886)
NAXIA IPIPHILCA			
Piper areanum	Piperaceae	Costa Rica	Marquis in DeVries (unpub)
Vitex cooperi	Verbenaceae	Costa Rica	DeVries (unpub)
PARAËNA			
Isertia longiflora	Rubiaceae	Brasil	Moss (1933)
Remijia amazonica	Rubiaceae	Brasil	Moss (1933)

Table 3. (continued)

Adelpha species/ foodplant	Plant Family	Locality	Reference
nr. paraëna			
Combretum decandrum	Combretaceae	Panamá	Aiello LOT 82-55
phliassa			
Alibertia edulis	Rubiaceae	Brasil	Moss (1933)
Bertiera guianensis	Rubiaceae	Brasil	Moss (1933)
phylaca aethalia			
Cecropia obtusifolia	Cecropiaceae	Panamá	Aiello LOTS 82-39, 82-68, 82-76, 83-78
Cecropia peltata	Cecropiaceae	Panamá	Aiello LOT 81-70
Cecropia peltata	Cecropiaceae	Panamá	Coley LOT 5
Cecropia sp.	Cecropiaceae	Panamá	Aiello LOT 82-40
plesaure			
Bathysa? sp.	Rubiaceae	Brasil	Müller (1886)
pseudococala			
Sabicea aspera	Rubiaceae	Brasil	Moss (1933)
pseudococala? (as nr. *cocala*)			
Sabicea sp.	Rubiaceae	Brasil	Müller (1886)
salmoneus			
Sabicea panamensis	Rubiaceae	Panamá	Aiello LOTS 82-37, 83-14
serpa			
Miconia minutiflora	Melastomataceae	Brasil	Moss (1933)
Misc. spp.	Melastomataceae	Brasil	Müller (1886)
serpa hyas			
Ilex paraguariensis	Aquifoliaceae	Barsil	cited in Lima (1968)
sophax (= *zalmona zalmona*)			
syma			
Rubus fructicosus	Rosaceae	Brasil	Müller (1886)
Rubus?sp. ("bramble")	Rosaceae	Brasil	Jones & Moore (1882–3)
Cephalanthus sarandi	Rubiaceae	Brasil	cited in Lima (1968)
thesprotia?			
Alternate-leaved climber	?	Brasil	Moss (1933)
tracta			
Undetermined	Rubiaceae	Costa Rica	Haber, Chacon in DeVries (unpub)
zalmona zalmona (as *sophax*)			
Sabiceae aspera	Rubiaceae	Costa Rica	DeVries (unpub)

reared on *Vitex,* has been found on only one other plant species (*Piper,* Piperaceae).

Pupa

Adelpha pupae (Figures 5 & 6) are diverse in form, yet have several features in common:

(1) The body is slender and tapers towards the cremaster, so that the posterior wing margins protrude and appear as keels.

(2) Segments T2 and A2 are expanded dorsally to form two projections of varying shape and size.

The thoracic projection is the smaller of the two and may be pointed and directed posteriorly (*A. salmoneus, cytherea, iphicla, justina*), or pointed and oriented almost perpendicularly to the body (*A. melanthe, phylaca aethalia*), or it may be reduced to a slight hump (*A. celerio*), or smooth curve (*A. basiloides*).

The abdominal projection is the larger and more variable of the two. It may be short, pointed, and directed anteriorly (*A. basiloides, justina*), a bit larger and curved anteriorly (*A. iphicla, celerio, cytherea, cocala*), even larger and directed posteriorly (*A. salmoneus*), or it may be a huge laterally flattened hook (*A. melanthe, phylaca aethalia*).

(3) The head usually has a pair of apical projections ("horns") of varying shape and size. These may be long, slender, and slightly curved (*A. celerio*), sickle-shaped and recurved to the sides (*A.*

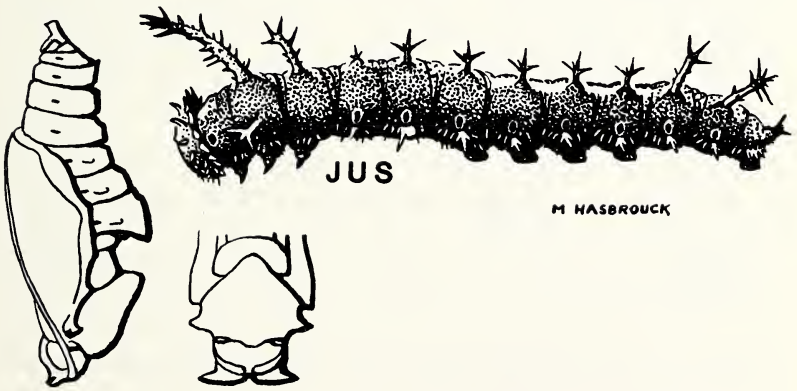

Figure 5. Final instar larva and pupa of *Adelpha justina justina,* (JUS) reared in Panamá.

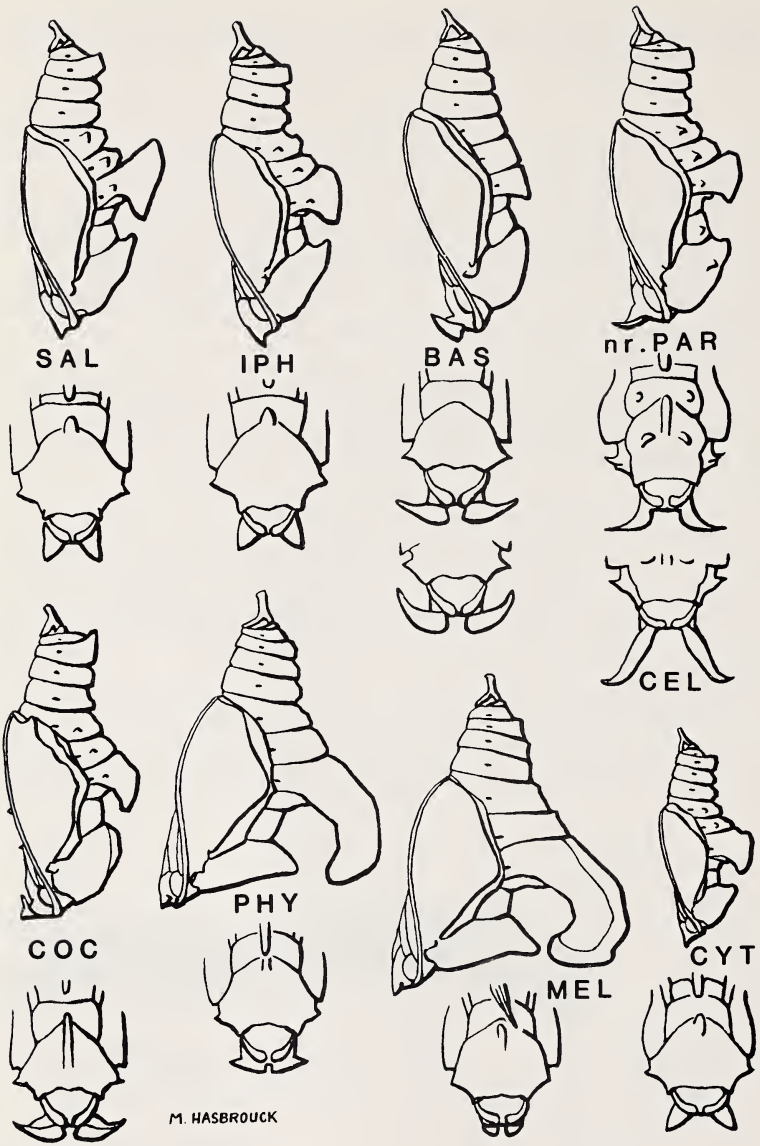

Figure 6. Pupae of *Adelpha* species reared in Panamá: abbreviations are the same as in Figures 2 & 4; CEL = *celario*.

basiloides), shaped like tiny asymmetrical leaves (*A. cocala, leucophthalma*), small and triangular, like cat ears (*A. iphicla, cytherea, salmoneus*), smaller triangles which are bent to the sides (*A. justina, phylaca aethalia*), or they may be reduced to two tiny rounded projections (*A. melanthe*).

(4) Pupal color varies from pearly white, through straw-color, brown, green, copper, or shimmering gold or silver. Whatever its color, an *Adelpha* pupa gives the impressing that it is empty or diseased. The pearly white pupa of *A. basiloides* is especially deceptive; it appears more to be an abandoned skin than a solid object. The shimmering silver pupae of *A. celerio* and nr. *paraëna* have black sutures and both give the impression that they are transparent with black lines showing through from the other side. As far as I know, the only other instance of a totally silver pupa occurs in *Mechanitis* of the Ithomiidae. The pupa of *A. salmoneus* is coppery brown and resembles a dead or diseased individual.

Adelpha Species Groups

In exploring for possible correlations between pupal and larval types, I began with species whose pupae have a large flat hook-like projection from the dorsum of A2. As it turned out, all have similar larvae, foodplants, and adult male genitalia, yet, the adult wing patterns are diverse. Further analysis revealed several other species groups that show similar correlations. Based upon this work, I have come to the conclusion that the genus *Adelpha* comprises five to seven natural groups, and possibly more. The only set of characters that doesn't hold together within these groups is adult wing pattern.

Some twenty species, for which adequate illustrations are available, are included in the classification which follows, and several others whose immatures were described only, are discussed.

The outline and discussion of *Adelpha* species groups includes brief final instar descriptions for species reared by me in Panamá, as well as comments upon previously published accounts of other species belonging to these groups. The MAJOR CHARACTERISTICS listed at the beginning of each group do not function as a key, rather, they represent defining characters for those groups, except as noted in parentheses. FOODPLANTS may host more than one butterfly group: members of GROUPS I and II have been reared on plants from

a number of families, GROUP III on Verbenaceae, and the remaining GROUPS (IV–VII) on Rubiaceae.

At this stage of our knowledge, an attempt to work out a phylogeny within *Adelpha* would be premature indeed; more information on life histories of *Adelpha* and its relatives (especially Old World genera) would be necessary to such an undertaking.

*KEY TO *ADELPHA* SPECIES GROUPS BASED UPON FINAL INSTAR LARVAE, PUPAE, AND FOODPLANTS

A. LARVA: body scoli, especially scolus of A2, flattened and feather-like; face with dark stripes. PUPA: shimmering silver with slender, very slightly twisted horns. FOODPLANTS: non-rubiaceous. (*A. celerio,* sp. nr. *celerio, serpa, paraëna*)

A. LARVA: body scoli not flattened or feather-like; face patterned or plain, but not striped. PUPA: perhaps with some metallic portions, but not totally metallic; head horns, various ... B

B. LARVA: scoli of A2–8 of similar form, although those of A2, and/or 7 & 8 may be longests. FOODPLANTS: non-rubiaceous C

C. LARVA: pale grey or pale brown with sides of thorax through A2 much darker than rest of body; scolus of A2 long. PUPA: with huge, hook-like dorsal projection from A2; head horns various..... .....(*A. phylaca aethalia, melanthe, isis, mesentina, delphicola,* (?)*calliphiclea,* (?)*abyla*)

C. LARVA: dark, or not patterned as above; scolus of A2 short. PUPA: hangs tilted with ventral side superior; head horns short points bent sharply to sides..... .....(*A. justina, jordani*)

B. LARVA: scolus of A2 different in form from scoli of A3–6 (in *A. iphicla* the difference is merely the swelling at base of A2 scolus) FOODPLANTS: rubiaceous..... D

D. LARVA: scoli of T2 or 3, and A2 & 7 swollen at base; (in *A. iphicla,* T2 & A2 only); face not patterned; head chalaza-1 not darker than others (don't known for *A. pseudococala*). PUPA: horns small, triangular "cat-ears" ..... E

*The reader should bear in mind that in all *Adelpha* species, the scoli of T1 and A2 are tiny.

E. LARVA: scoli of A2 conical, close together, and with fewer spines at base; scoli of A3–6 very short ..... (*A. cytherea, salmoneus, pseudococala*)

E. LARVA: scolus of A2 not conical, similar to other scoli except for its swollen base; scoli of A3–6 of moderate length; face smoother than other species due to reduction or loss of most chalazae ..... (*A. iphicla*)

D. LARVA: body scoli about same thickness at middle as at base; scolus of A2 strongly arched towards the posterior, thick and densely spined; face patterned; head chalaza-1 dark, and chalazae-3 & 4 pale compared to rest of face. PUPA: head horns curved or recurved to sides ..... F

F. LARVA: scoli of T3 and A7 long, slender, and tapered to sharp point; scoli of A7 & 8 differ in form from each other (that of A8 club-shaped). PUPA: head horns sickle-shaped ..... (*A. basiloides, phliassa*)

F. LARVA: body scoli not tapered to sharp point; scoli of A7 & 8 similar in form. PUPA: head horns like tiny asymmetrical leaves ..... (*A. cocala, leucophthalma*)

GROUP I

MAJOR CHARACTERISTICS:

(1) Larval body scoli flattened;
(2) Larva with face striped;
(3) Larval head chalaza-1 dark (also true of GROUPS VI & VII);
(4) Larvae assume a curled resting position;
(5) Pupa shimmering silver;
(6) Valves of male genitalia without clunicula;

FOODPLANTS: Aquifoliaceae, Bombacaceae, Cecropiaceae, Combretaceae, Melastomataceae, Rubiaceae, Urticaceae.

Two larval types have been observed within this group:

A. Final instar larvae with A2 scolus broad, curved posteriorly, and with median spines spreading ..... nr. *celerio, serpa.*

A. Final instar larvae with A2 scolus longer, slender, straight (although directed posteriorly), and with median spines ascending ..... *celerio, paraëna*

Pupae vary only slightly, the more apparent differences being in the length, and degree of curvature of the head horns, and in the shape of the dorsal projections on T2 and A2. Head horn shape and size do not appear to correlate with the two larval types seen so far, and perhaps varies even within a species.

celerio, Panamá (Aiello, Coley)

Larvae are dark, mostly black above and green laterally, with pinkish lateral spots on A2–4, 7 & 8; scoli on thorax and A7 & 8 are pale, while that of A2 is black; subspiracular scoli A2–4 are mixed pale lime and bright green. A black subspiracular stripe passes along the thorax and turns sharply upward across A1 and fuses with the dark scolus of A2. A few days before pupation the pinkish lateral marks change to green, as do the scoli of T3 and A7 & 8; the scolus of A2 remains dark. Just prior to pupation larvae fade to a dirty yellow. Larvae rest in the curled position with the posterior end elevated and the white undersurface of A8 & 9 exposed, and in this configuration resemble a bit of fallen moss and lichen mingled.

Pupal head horns are long, and slightly curved near their tips. Adults resemble *iphicla* in wing pattern.

nr. *celerio,* Panamá (Aiello)

A larva resembling *celerio* produced, but with the A2 scolus short and broad, a pupa that had short head horns and appeared identical to my nr. *paraëna.*

Unfortunately the pupa died and its identity remains a mystery.

celerio diadematа, Mexico (Comstock & Velazquez, 1960)

The illustrations of this larva and its pupa indicate membership in GROUP I; the larva is clearly of the *celerio* type having long narrow scoli, even on A2. The pupa closely resembles that of the *celerio* reared by me in Panamá; the head horns are long and slightly curved just before their tips.

The authors report that their larva faded to yellow just before pupation.

paraëna, Brasil (Moss, 1933)

From its illustration, the larva of this species is of the slender scolus type. Moss noted that it was brighter green than *serpa* and had none of the orange spines. The record of Rubiaceae for *paraëna* is unique for this group.

nr. *paraëna,* Panamá (Aiello)

In pattern, this larva is very similar to *A. celerio,* but is paler above, being mottled brown and black, with a white dorsal patch joining A6 & 7. The scoli are brown, that of A2 being the darkest; subspiracular scoli A2–4 are pink. The larva turned yellowish just prior to pupation.

The pupal head horns are shorter than those of *celerio,* and curve outward at about their midpoint.

Adults resemble *celerio* so closely that I did not realize they were different species until rearing them, and doubtless they are mingled in many collections.

serpa, Brasil (Moss, 1933)

The larva of *serpa* has the scolus of A2 shorter and denser than the other major scoli, and I take it to be of the same general type as *celerio.* Moss described the scolus of A2 (segment 6 in his system) as being bushy and dark green, and the other major scoli as ochreous (orange). His larva rested with the anterior portion turned, and resembled a bird dropping.

serpa, Brasil (Müller, 1886)

Müller's illustrations of *serpa* show the larval face, and a scolus from A2. The face is clearly striped, and the scolus is short, thick, and has flattened spines overlapping each other; each of these conditions of the scolus is more extreme than in nr. *celerio.*

GROUP II

MAJOR CHARACTERISTICS:

(1) Larva pale, with sides of thorax through A2 darker than rest of body;
(2) Pupa with huge, laterally flattened, hook-like projection from dorsum of A2;
(3) Pupal head horns diverse: leaf-shaped, bent triangular, rounded;

(4) Valves of male genitalia armed with row of teeth beginning at apex and extending along lower edge; clunicula broad;

FOODPLANTS: Aquifoliaceae, Bombacaceae, Cecropiaceae, Ulmaceae, Urticaceae.

abyla, Jamaica (Swainson, 1901)

There are several things in Swainson's description that lead me to place *abyla* tentatively with GROUP II. "On first segments are two brown horns with sharp points bending over the head; from this to the end of the third segment is silvery grey; then two tiny horns bending backward." "The [pupa] shape is very curious, resembling the pictures of 'Punch,' long nose and all." It appears that larval segments T1 and A1 were overlooked, probably because of their small size and tiny scoli. The silver area would then be bounded by scoli of T2 and A2, suggesting the two-toned larva of GROUP II. The pupal description may be in reference to the long abdominal hook of GROUP II, or it may be an overreaction to the shorter dorsal projection of a species in some other group (*iphicla* perhaps). Unfortunately, no foodplant is mentioned.

calliphiclea, Paraguay (Jorgenson, 1921)

Jorgensen's description of the pupa as having the abdomen prolonged toward the thorax, forming a large hook, induces me to place *calliphiclea* in GROUP II: "El torax arriba con una carena alta como el abdomen en el dorso este ultimo hacia el torax prolongado, formando un gran gancho." In addition, the non-rubiaceous foodplant (*Ilex*) is consistent with this group.

Each of the five species remaining, possess characteristics 1 & 2 above, and there is no doubt in my mind that they are all close relatives. Pupal head horn shape may have taxonomic value within the group but that cannot be determined until a larger number of species has been reared.

delphicola, Brasil (Moss, 1933)

The pupal head horns curve to the sides and resemble tiny asymmetrical leaves; the hook on dorsal A2 is rounded at the tip.

isis, Brasil (Müller, 1886).

Müller's illustration of the pupa is a lateral view so the head horn shape does not show, however, it is stated in the text that

the horns are small points bent to the sides. The hook on A2 is enlarged slightly at the tip much as in *melanthe.*

melanthe, Panama (Aiello)

The larva is grey (darker above) excepting the dorsal thorax through A2, which is dirty yellow, and the sides of that same area, which are dark brown. The scoli are grey with black spine bases and apices. The larva has a frosted appearance partly due to its patterned scoli, but mostly because the entire body is densely clothed with short thick grey setae. It is the only *Adelpha* species so far that has rounded pupal head horns. The hook on A2 is slightly expanded at the tip.

Adults of *melanthe* look like large *salmoneus* but the undersurface is quite different.

mesentina, Brasil (Moss, 1933)

From Moss's illustrations, *mesentina* and *delphicola* larvae are similar, and no doubt these two species are close relatives. As a result of their close resemblance, Moss did not realize that he had two species until the adults emerged. If his illustrations are accurate, then *mesentina* has a less rounded pupal hook than *delphicola,* but the head horns are nearly the same.

phylaca aethalia, Panamá (Aiello, Coley)

The larva is greenish or pinkish grey, and speckled with darker grey (especially on the dorsum); the sides of the thorax through A2 are dark brown, and some individuals have a dark brown oval on each side of A5, just below the scolus. Pupal head horns are short triangles bent to the sides.

Adults are very close look-alikes of *cocala.*

GROUP III

MAJOR CHARACTERISTICS:

(1) Larval scoli A2–6 all similar and short;
(2) Pupa tilted so that ventral side is superior (at least in *justina*);
(3) Pupal head horns small triangles bent to sides (also occurs in GROUP II);
(4) Valves of male genitalia unarmed (also true of GROUP IV);

FOODPLANTS: Verbenaceae.

The most interesting thing about this group is the fact that the scolus of A2 is just the same as those of A3–6. Both species, thus far included, rest in the front-curved position, as shown in Moss's illustration of *jordani*. Also in both, the pupal dorsal A2 projection is a short point, directed anteriorly, and the T2 projection is smaller.

This and GROUP IV have similar genitalia, but feed on different foodplant groups. I see them as close but distinct relatives.

jordani, Brasil (Moss, 1933)

The larva is dull green with black-spined, orange scoli; the pupa is white with black spots.

justina, Panamá (Aiello & Small)

Early final instar larvae are dark brown (lighter dorsally) with paler scoli (black at tips of those on T2 and A7 & 8), but later change to black and white checkered with transverse orange bands joining members of scolus pairs (A2–8).

The straw-colored pupa has a dorsal metallic sheen, from head through A1, and lacks the prominent spotting of *jordani*.

Adults of *justina* closely resemble *leucophthalma* and the two can be found flying together.

GROUP IV

MAJOR CHARACTERISTICS:

(1) Larva with scoli of A2 conical, close together, and with fewer spines at base;
(2) Larval face with chalazae reduced in size;
(3) Pupal head horns of this and Group V, are small, triangular "cat-ears;"
(4) Valves of male genitalia unarmed (also true of GROUP III);

FOODPLANTS: *Sabicea* (Rubiaceae).

nr. *cocala,* Brasil (Müller, 1886)

The larva illustrated does not at all resemble that of *cocala,* so I guess Müller's label "bei *cocala*" to have been based upon adult appearance. Like *cytherea,* this larva shows the conical scolus of A2, the thick based scoli of T2, and A7, and the very short scoli of A3–6. As well, Müller's larva fed on *Sabicea.*

cytherea, Brasil (Moss, 1933)

Of this larva, Moss commented, "Now in two shades of brown, on the stem or near flower-head easily mistaken for a part of the plant...."

cytherea marcia, Panamá (Aiello)

The larva is patterned dark and light brown; with dark brown, oblique lateral stripes, which cross segments A3–8. A thin white subspiracular line expands into a lime-green mark on A7–9.

The pupa is straw-color but takes on a silver or gold sheen at certain angles.

pseudococala, Brasil (Moss, 1933)

Moss states merely that the larva of this species is identical to *cytherea,* although larger and greener at the ends.

The pupal abdominal projection is directed towards the posterior as in *salmoneus.*

salmoneus, Panamá (Aiello)

The dark brown second through fourth instar larvae, with their grey, oblique, lateral stripes, are well camouflaged amongst the dark, pale-veined, young leaves of their foodplant. Fourth and fifth instars have red-brown heads.

Early final instar larvae are brownish green, and become greener with age. By late final instar, larvae are bright yellow-green; the dorsal area of A4 & 5 is pale purple-brown; A4 & 5 each bear a dark lateral purple mark; the head is red-brown; scoli of T2 & 3, and A2 & 7 are brown-purple, while that of A8 is still green.

The pupa is bronze with dorsal gold, and has an A2 projection that is prolonged more towards the posterior end than the anterior.

Group V

MAJOR CHARACTERISTICS:

(1) Larval scoli of T2 and A2 swollen at base, otherwise, all body scoli usually similar in form;

(2) Pupal head horns of this and GROUP IV, are small, triangular "cat-ears";

(3) Larval head uniformly dark, and face smooth except for usual pits, and two pairs of reduced chalazae (nos. 2 & 4);

(4) Valves of male genitalia armed with apical row of teeth which extend to outside of valve;

FOODPLANTS: *Antirrhoea, Alseis, Bathysa, Calycophyllum, Gonzalea, Isertia, Rondeletia, Uncaria* (Rubiaceae).

iphicla, Panamá (Aiello)

The color of *iphicla* larvae varies from dark grey, through golden brown, and red-brown, to almost black, regardless of the foodplant eaten. The head is always smooth (by *Adelpha* standards) and also varies, from yellow-brown with black punctations to uniform dark brown or black. Final instar larvae show the most pattern (especially light-colored individuals): dark, oblique lateral stripes on A2–5, which terminate part way up the bases of the scoli, and often but not always, white lateral marks on A2, 7 & 8.

The pupa varies from waxy white to straw-color or pale brown, and often is partly or entirely burnished gold or silver, especially on dorsal T1 & 3, and A1. Almost always there is a small silver diamond located on the base of each mesothoracic leg.

iphicla, Brasil (Moss, 1933)

Moss described *iphicla* larvae as "very similar to *cytherea,* the two species evidently being closely related, as is also shown by the pupae."

GROUPS IV and V may be related; the "cat-eared" pupae, and oblique-striped larvae of both, seem to hint at that. As well, both groups of larvae display varying degrees of reduction of head chalaze, and swelling of certain scoli bases. However, the genitalia of the two groups are different, and, in *iphicla* the scoli on A3–6 are longer and the face smoother than in Group IV. And so, for the moment they will be kept separate, but near to each other.

GROUP VI & VII

MAJOR CHARACTERISTICS:

(1) Larva with scolus of A2 arched towards the posterior, thick, and densely spined;
(2) Larval face patterned;
(3) Larval head chalza-1 dark (also true of GROUP I);

(4) Valves of male genitalia armed with apical row of 2–6 fairly uniform teeth;
(5) Larval head chalazae 3 & 4 pale, and contrasting with face.
FOODPLANTS: Rubiaceae.

These two groups are very closely related and perhaps will be merged when more is known of their larval and pupal diversity. For now they are placed apart on account of the specialized scoli in *basiloides,* and differences in the form of the pupal head horns.

GROUP VI

ADDITIONAL CHARACTERISTICS:
(5) Larval scoli of T3 and A7 long, slender, and tapered to sharp point;
(6) Larval scolus of A8 club-shaped;
(7) Larval face pattern, independent of pits;
(8) Pupal head horns sickle-shaped;
FOODPLANTS: *Alibertia, Amaioua, Bertiera, Ixora* (all Rubiaceae).

basiloides, Panamá (Aiello)

Larvae are mottled black and brown, and are paler towards the posterior end. The dark and pale portions intersect obliquely along a line beginning at the subspiracular scolus of A4, and terminating dorsally at the beginning of segment A7. The dorsal dark portion thus comes to a point at the beginning of A7. As larvae approach pupation, they may become tinged with rose or green, especially at scoli bases, and laterally on A4–6.

The pupa is pearly white with black tiped head horns, and appears empty. Head horns vary somewhat in length and degree of curvature, even among larvae collected on the same plant. Both extremes are illustrated (Figure 6).

phliassa, Brasil (Moss, 1933)

Comparing my observations of *basiloides* with Moss's description and illustrations of *phliassa,* it appears that the two are extremely close relatives.

plesaure, Brasil (Müller, 1886)

The pupa illustrated appears identical to those of *phliassa* and *basiloides.* Hall (1938) feels that *plesaure* and *phliassa* are one and the same species.

GROUP VII

ADDITIONAL CHARACTERISTICS:

(4) Larval face pattern due to dark pits against a paler face;
(5) Pupal head horns shaped like tiny asymmetrical leaves (also occurs in GROUP II);

FOODPLANTS: *Calycophyllum, Chomelia, Malanea, Pentagonia, Psychotria, Uncaria, Warscewiczia* (all Rubiaceae).

cocala, Panamá (Aiello)

Early fifth instars are crypticaly patterned with golden brown and black; later the pattern remains but the colors become moss-green, black, and cream, and a pinkish grey and black area appears on dorsal A3–6, plus a broad, oblique, lateral pinkish or yellowish stripe across A4 and 5 together. Some individuals have a subspiracular lime-green mark on each of A7 & 8.

The pupa is dark green.

cocala, Brasil (Moss, 1933)

The curved, thick scoli of A2 show clearly in Moss's illustration, but his larvae had more than one lateral oblique stripe. The pupae appear nearly identical.

His record of *Emmotum* (Icacinaceae) as a foodplant, in addition to *Malanea* (Rubiaceae) is odd, and is the only reported deviation, by *cocala,* from Rubiaceae.

leucophthalma leucophthalma, Panamá (Aiello & Small)

The larva of *leucophthalma* is apparently indistinguishable from that of *cocala* (G. Small, personal communication) and the two species must be closely related.

The pupa also is very similar to *cocala,* but differs in being brown or copper-color, and in having the abdominal projection rather square, the thoracic projection more pointed, and the head horns farther appart at their bases.

leucophthalma leucophthalma (as *l. tegeata*), Costa Rica (Young, 1974)

The observations by Young are consistent with those of Gordon Small and myself.

SPECIES EXCLUDED FROM THIS CLASSIFICATION

erotia, Brasil (Müller, 1886)

An isolated scolus, figured by Müller and labelled *erotia,* would

place that species in GROUP I, but I would like to see more evidence. In addition, the *erotia* wing-undersurface pattern does not have the sharply stamped appearance typical of GROUP I, and it is possible that the butterly was misidentified.

iphicla iphicleola, Mexico (Comstock & Vazquez, 1960)
This record was in error; the authors misidentified *Doxocopa* as *Adelpha.*

melona, Brasil (Moss, 1933)
The larval description and illustrations in Moss do not give sufficient detail to place this species, although from the pupa it belongs in GROUP VII.

thesprotia, Brasil (Moss, 1933)
The larval description and illustration in Moss do not give sufficient detail to place this species, although I suspect that it may represent an eighth group. As well, there is a good deal of disagreement concerning the identity of Moss's *thesprotia;* Forbes (unpublished) believed that Moss actually had *nea*, a species which on the basis of genitalia probably belongs to GROUP I. Moss's statement that the larva rested in a curled position (typical of GROUP I), lends support to Forbe's suspicion. However, from what can be seen of the scoli in Moss's illustration, they are all similar in size and form, are not flat, and the pupa looks more like those of GROUP VIII.

Significance of Adult Wing Pattern

When adult specimens of *Adelpha* are sorted into the species groups just outlined, the result is a jumble of wing pattern types that would make any biologist wince, this author included. However, it would seem even less natural to split groups that are based upon the presumably more conservative characters of the immatures. I prefer to think that in *Adelpha,* wing pattern not only does not reflect species relationships, but instead may be intended to deceive. One might expect adult wing characters to be the most specialized and difficult to interpret; adults move about with ease and interact with each other and with other butterfly species, as well as with potential predators, while in most cases the immature stages must contend, in

a less active way, with predators and parasites alone. An explanation of *Adelpha's* wing pattern madness, might be that this genus is comprised of several groups, of various affinities, which together form a large mimicry complex, perhaps based upon members whose larvae feed on alkaloid-bearing plants (e.g., Rubiaceae). Possible examples are found among the unrealted look-alikes reared by me in Panamá (Figure 7): *phylaca aethalia* (non-rubiaceous feeder (NR)) closely resembles *cocala* (rubiaceous feede (R)); *justina* (NR) resembles *leucophthalma* (R); *melanthe* (NR) is larger than, but very similar in pattern to *salmoneous* (R); and *celerio* and nr. *paraëna* (both NR) are very similar in pattern to *iphicla* and *basiloides* (both R). The idea is intriguing, but must be labelled "pure speculation" until data on palatability of *Adelpha* butterflies is available. In its defense, however, I would like to point out that there are several examples of *Adelpha* look-alikes in uncontestably unrelated butterflies. *Nymula velabrum* (Riodinidae), whose wing pattern closely resembles that of *A. iphicla,* and several other *Nymula* species that are look-alikes of other *Adelpha* types, all depart from the basic wing pattern of their genus. Female *Doxocopa laure* and *pavon* (Nymphalidae) resemble *A. iphicla,* while female *D. clothilda* are even more convincing look-alikes of *A. salmoneus.* Male *Doxocopa clothilda* and *pavon* differ from the females of their species, and do not resemble *Adelpha,* while the male of *D. laure* has an *Adelpha*-like wing pattern with overlying purple iridescence. *Pyrrhogyra hypsenor* (Nymphalidae) is similar in appearance to *Adelpha* species that have broad white bands, and has fooled at least one lepidopterist (Muyshondt, 1974).

Old World Relatives

The few published accounts of life histories for Old World Limenitidinae provide intriguing glimpses into the trove of information awaiting the attention of lepidopterists. Many larval and pupal forms, similar to those of *Adelpha,* occur among Old World genera, and in addition, many utilize the same foodplant genera as *Adelpha* and display similar larval behavior. Life history studies, that compare Old and New World groups, are essential to our understanding of generic limits and relationships within this subfamily.

[6]Morrell (1954) gives a fascinating account of larval behavior in several Malayan genera of the tribes Limenitidini *(Athyma, Moduza, Pandita)*, and [7]Neptini *(Lasippa, Neptis, Phaedyma).* Except for *Neptis leucoporos,* the larvae, of the butterflies he observed, expose the midrib, or a secondary leaf vein, by feeding around it (just as *Adelpha* does); young larvae rest out on these slender supports. Like *Adelpha* also, *Athyma, Moduza,* and *Pandita* accumulate their feces to form a mass at the base of the support vein; Neptini do not.

Judging from Morrell's illustrations, the larva of *Moduza* resembles a combination of *Adelpha cocala* and *basiloides,* especially in having short thick scoli on A2; its pupa is remarkably like *A. cocala* or *leucophthalma,* but with slightly stalked head horns; the host plants are mainly Rubiaceae *(Mussaenda, Nauclea, Timonias, Uncaria, Wendlandia),* with one record on Oleaceae *(Olea).*

The larvae of *Athyma kanwa* feeds on *Uncaria,* and is described by Morrell (1960) as "brown with delicate green branched spines, and resembles a growth of moss on a decaying patch of leaf;" the pupa (illustrated in Morrell, 1954) is silver with long head horns and to me looks for all the world like a pupa of *Adelpha celerio.*

In form, *Athyma nefte* larvae (Morrell, 1954) are reminiscent of a very plump *Adelpha iphicla* larva, and have been reported on *Glochidion* (Euphorbiaceae) and *Mussaenda* (Rubiaceae); the pupa is "golden brown in colour, with two dorsal plates of brilliant metallic gold," and from what can be determined from its picture, it looks like the pupa of *Adelpha iphicla* or *cytherea,* but with an exagerated A2 projection, and like those species it appears to have short pointed head horns.

Pandita sinope is described by Morrell (1954) as having a larva similar to that of *Athyma nefte* in color and general appearance; the illustration of the pupa is also similar to *A. nefte,* but has a less

[6]According to Corbet and Pendlebury (1978), five of the seven names used by Morrell (1954) should be amended: his *Neptis columella = Phaedyma columella; Neptis heliodore = Lasippa tiga; Neptis nata = Neptis leucoporos; Parathyma kanawa = Athyma kanwa; Parathyma nefte = Athyma nefte.* His *Moduza procris* and *Pandita sinope* remain unchanged.

[7]Neptini is defined by Eliot (1969) to include *Aldania, Lasippa, Neptis, Pantoporia,* and *Phaedyma.*

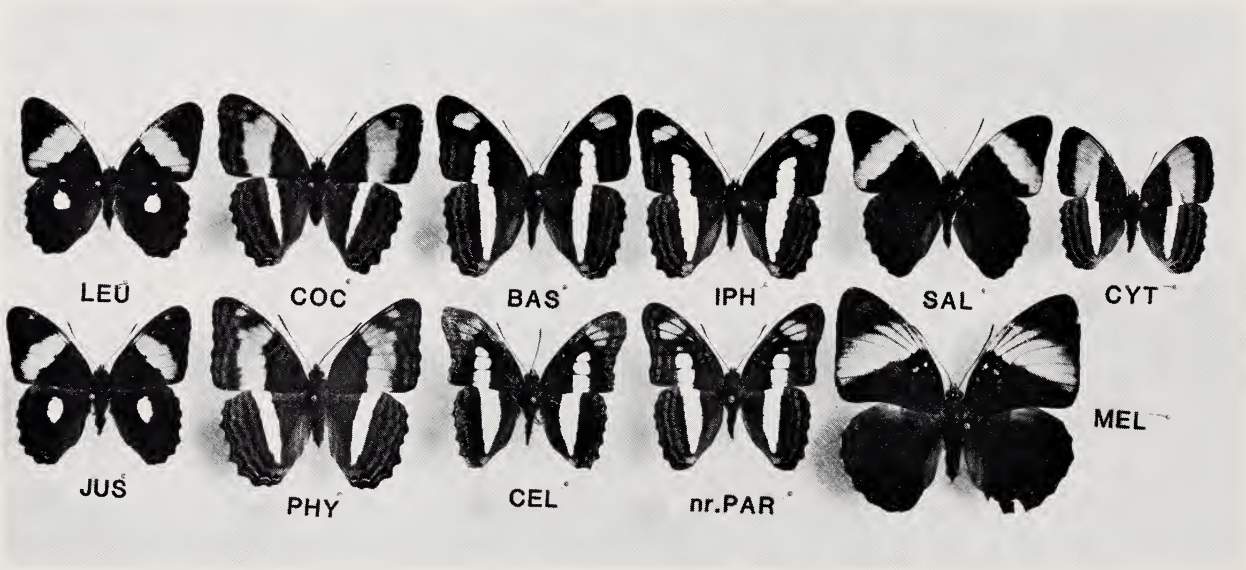

Figure 7a. Upper and lower surfaces of adult Adelpha species reared in Panamá: BAS = *basiloides,* CEL = *celerio,* COC = *cocala,* CYT = *cytherea marcia,* IPH = *iphicla,* JUS = *justina,* LEU = *leucophthalma,* MEL = *melanthe,* nr. PAR = *near paraëna,* PHY = *phylaca aethalia,* SAL = *salmoneus.* Species in the upper row are rubiaceous feeders as larvae, whereas larvae of those in the lower row feed on various non-rubiaceous plants.

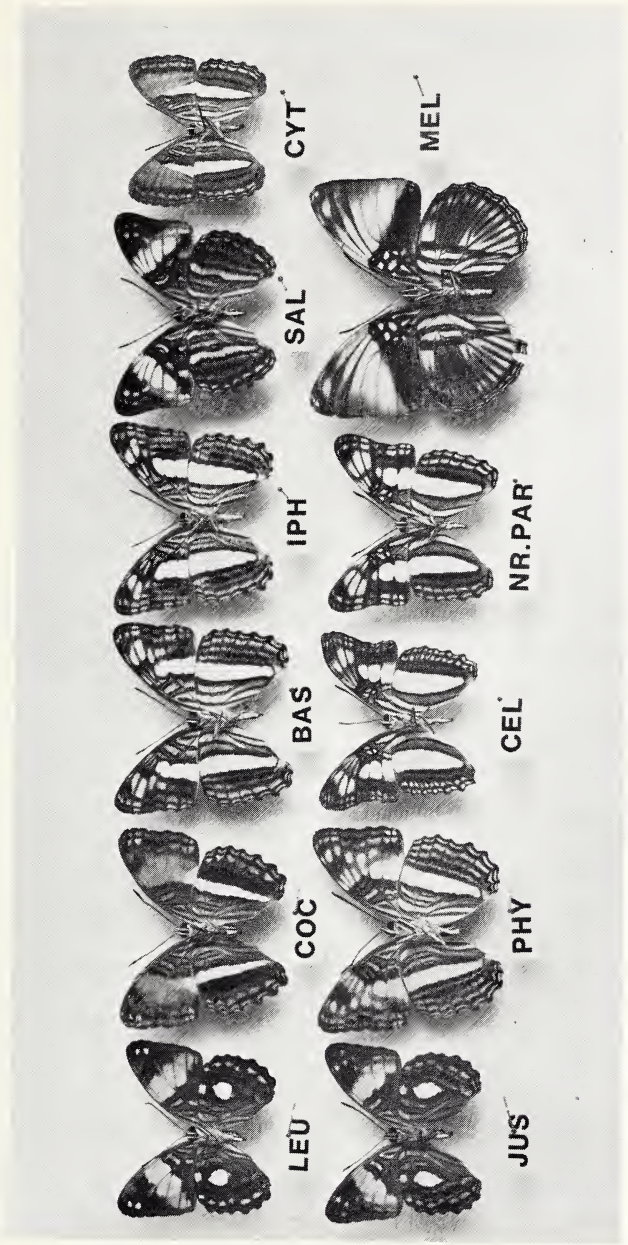

Figure 7b. Lower surfaces of adult *Adelpha* species reared in Panamá. Abbreviations as in figure 7a.

exagerated A2 projection and thus appears almost identical to pupae of *Adelpha iphicla* and *cytherea*. Larvae of *P. sinope* feed on *Uncaria* (Rubiaceae).

The valves of the male genitalia in *Pandita sinope* and *Athyma nefte* are unarmed, have cluniculae, and look very similar to those of *Adelpha* GROUPS III & IV.

A number of other life history accounts for Old World Limenitidini have been published, but it is not the intent of this paper to report them in detail. Instead, I merely wish to point out a few of the intriguing similarities that exist between Old and New World groups, in hope of prompting other workers to investigate this promising group.

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EARWIGS OF THE CALIFORNIA CHANNEL ISLANDS, WITH NOTES ON OTHER SPECIES IN CALIFORNIA (DERMAPTERA)*

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Although the earwigs of the California Channel Islands were included in Langston and Powell (1975) and Langston and Miller (1977), newly accumulated records extend their distributions significantly (Table 1). Some of these new records are due to increased collecting activity by interested entomologists, but most probably represent range expansion by the earwigs, aided by increased human activity on the islands. The two species involved, *Euborellia annulipes* (Lucas) (Carcinophoridae) and *Forficula auricularia* Linnaeus (Forficulidae), are both considered to be introduced to California (Langston and Powell 1977). The two are readily distinguished by the shape of the forceps (Langston and Powell 1977: figs. 3, 11), as well as the adults being wingless (*E. annulipes*) or winged (*F. auricularia*). This note is based on the collections of the California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (LACM), Peabody Museum of Yale University, San Diego Natural History Museum (SDNHM), Santa Barbara Museum of Natural History (SBMNH), Smithsonian Institution (USNM), and University of California at Berkeley (UCB), as well as my own fieldwork on all islands from 1976 to 1984.

Euborellia annulipes (Lucas)

This cosmopolitan species has been established in coastal southern California since at least the 1880s (Langston and Powell 1977). Channel Islands records are as follows: *Santa Rosa:* A single female was taken in July 1939 (LACM). A colony was found at Johnsons Lee in May 1977 (SBMNH). *Santa Catalina:* A series was collected at Avalon in October 1908 (USNM), but recently only single indi-

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viduals have been collected at Catalina Harbor (July 1979, LACM) and on the beach at Toyon Bay (May 1981, SBMNH). *San Clemente:* A series was collected in 1885 or 1886 by T.L. Casey (USNM), one was collected in November 1941 (LACM), and it has been taken in the 1970s around Wilson Cove (military living compound) and the new airport.

Forficula auricularia Linnaeus

This cosmopolitan species has not been established in California as long as *E. annulipes* and has undergone rapid expansion of range in the state in the last fifty years (Langston and Miller 1977). It was probably not established in coastal southern California until at least the 1940s (Langston and Powell 1975). Channel Islands records are as follows: *Santa Rosa:* Colonies sampled during the 1970s at Beechers Bay (ranch headquarters), Arlington Canyon, and Wreck Canyon (CAS, SBMNH, USNM). *Santa Cruz:* Powell (1981) discusses the establishment of this species between the late 1960s and 1978. It is now well established in the Central Valley. *Santa Catalina:* Between 1975 and 1983, it has been collected at Catalina Harbor, Cherry Cove, Cottonwood Canyon, Gallaghers Beach, Parsons Landing, Twin Harbors (Cat Harbor), and Toyon Bay (LACM, SBMNH), and can be very abundant (S.G. Bennett pers. comm.). *San Nicolas:* Taken in 1980 and 1982 at the military living compound (LACM, SBMNH). *San Clemente:* First taken at the new airport in March 1972 (UCB), it was taken at Wilson Cove and Lemon Tank in December 1981 (SBMNH). *Santa Barbara:* One female taken in June 1983 (LACM).

Discussion

Both species are generally restricted to the areas around human activity (i.e. ranch and military facilities) and beaches. The earwigs are omnivorous, sometimes predaceous on other insects, often feeding on live or dead vegetation, often injuring crops on the mainland (Langston and Powell 1975). These species, especially *Forficula auricularia,* can also be household nuisance pests, and can cause considerable annoyance in large numbers.

Based on the data presented above, *E. annulipes* has been present on three islands for 40 to 100 years and maintains small popula-

Table 1. Summary of earwig distribution on the California Channel Islands.

Island	*Euborellia annulipes*	*Forficula auricularia*
San Miguel		
Santa Rosa	X	X
Santa Cruz		X
Anacapa		
Santa Catalina	X	X
San Nicolas		X
San Clemente	X	X
Santa Barbara		X

tions, probably near the sites of initial introduction by man. *F. auricularia,* however, has apparently become established on six islands, mostly during the 1970s. It has not yet been recorded from San Miguel and Anacapa islands, but should be expected there. The agencies which administer the islands should attempt to discourage the rapid expansion of *F. auricularia,* by preventing additional introductions and eradicating existing populations when possible.

Appendix

The following are significant additions to Langston and Powell (1975) and Langston and Miller (1977): Following Brindle (1971) and Steinmann (1975), the proper name of *Spongophora apicedentata* Caudell is *Vostox apicedentatus* (Caudell). *Euborellia femoralis* (Dohrn), a new California record, was reported from Red Hill Marina, Calipatria, Imperial County, by Steinmann (1981). *Forficula auricularia* has been established in the San Diego area, new southern record in California, since at least the mid 1970s (specimens in SDNHM).

Acknowledgements

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University of California at Santa Barbara Marine Science Institute for logistic and financial support of surveys; the curators of the collections consulted; and S.G. Bennett, P.W. Collins, F.G. Hochberg, C.L. Hogue, R.W. Klink, R.L. Langston, C.D. Nagano, J.A. Powell, H. Steinmann, and D.B. Weissman for specimens and assistance.

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NESTING BIOLOGY AND DEFENSIVE BEHAVIOR OF *MISCHOCYTTARUS (MONOCYTTARUS) MEXICANUS CUBICOLA* (VESPIDAE:POLISTINAE)*

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Introduction

Mischocyttarus mexicanus (de Saussure) is one of two species in this genus that occurs in the U.S. (Krombein *et al.,* 1979). This genus is primarily Neotropical, being treated taxonomically by Bequaert (1933), Richards (1945, 1978) and Zikán (1935, 1949).

Litte (1977, 1979) described the biology of *M. mexicanus* in Florida and *M. flavitarsis* (de Saussure) in Arizona. *M. m. mexicanus* is found in Texas, Mexico and other parts of Central America. *M. m. cubicola* to date has been found in Georgia, Florida, Alabama, Cuba and the Bahamas (Krispyn and Hermann, 1977; Krombein *et al.,* 1979).

Litte's study of the nesting biology and behavior of *M. m. cubicola* (Litte, 1977, then described as *M. mexicanus*) was carried out at Archbold Biological Station at Lake Placid in southern Florida (Highlands County) where weather conditions allowed the wasps to nest throughout the winter. Our primary study area in Georgia had a more temperate climate where a 3 to 4 month hibernation period was necessary.

Sapelo Island, a 14–mile-long barrier island in McIntosh County, Georgia, consists of Holocene and Pleistocene deposits (Duncan, 1982). There is no official weather station on Sapelo Island. However, the average annual rainfall from 1944 to 1964 at McKinnon Airport on the southern end of St. Simons Island, about 7 miles south of Sapelo, was 134.6 cm, with half of this falling during a 4-month period from June to September.

Mean minimum temperature for the coldest months was about 6.1° C (43° F). Temperatures as low as 0° C (32° F) occur only 15 days of the year. The lowest recorded temperatures were −10° C

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(14° F) in December, 1962, and −7.8° C (18° F) in February, 1958. Mean daily maximum temperature during the summer was under 32.2° C (90° F), only 49 days per year having a maximum of 32.2° C or above. The highest recorded temperature was 38.9° C (102° F) in June, 1950.

The purpose of this paper is to report the general nesting biology and defensive behaviors of *M. m. cubicola* at Sapelo Island.

Materials and Methods

Four trips were made to Sapelo Island (fall of 1982; late winter-early spring, 1983; June 9–12, 1983, August 23–30, 1983), one to Patterson Island, Ga. (adjacent to Sapelo) (June 11, 1983), one to Orlando, Polk County, Fla. (Aug. 7, 1983) and one to Haines City, Polk County, Fla. (Aug. 5–8, 1983). Two of the trips to Sapelo Island were preliminary surveys of the island while the later trips to Sapelo and the other three study areas revealed nests in various stages of development.

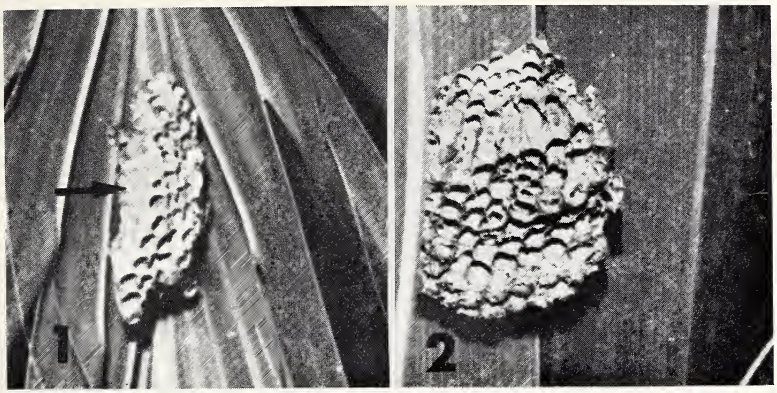
When an active nest was found, an attempt was made to provoke adults to defend by prodding them with the tip of a pen or comparable instrument. Defensive behaviors were video taped (Hitachi VT-650A VTR and VK-C600 color camera) during August so that they could be examined closely and repeatedly. Due to their readiness to escape under provocation in the early nesting season (June), some adults were lost. Following a study of their defensive behaviors, the nest and remaining adults were taken.

Nest contents and information on attending adults were later recorded. A comparison between paper surfaces of young and older nests was made through the use of scanning electron microscopy. Parts of nests were removed and adhered to specimen stubs with double-stick tape. They were coated with palladium-gold for 2 minutes in a Hummer sputter coater and observed with a Cambridge Mark II scanning electron microscope.

Results and Discussion

Nesting Sites

Nests of *M. m. cubicola* were found on buildings, other man-made structures and on vegetation. Nests on the former were most often found on the wooden frames of windows, on the wooden support beams of metal roofed outbuildings and on the underside of



Figures 1 and 2. Nests of *M. m. cubicola* at Sapelo Island, showing the general structure and safety area on the back of the nest (arrow).

concrete arbors. Small (5–15 cells) uninhabited nests (Figs. 1 and 2) were numerous on the wooden frames of windows of the R. J. Reynolds home adjacent to the Marine Institute dormitory at the southern end of the island. Uninhabited nests were also found less abundantly on wooden structures of other buildings at the island's south end. Nest abandonment at these locations was partially due to occasional sprayings of pesticides. Three nests were found in metal and ceramic bell-like wind chimes in the Haines City, Polk County, Fla., location.

Nests on vegetation on Sapelo Island were found only on the underside of the leaves (Fig. 3) of the cabbage palm, *Sabal palmetto* (Walt.). This tree and *Serenoa repens* (Bartr.) (the common saw palmetto) (Fig. 4) are the most predominant members of the palm family, Arecaceae (= Palmae), found on Sapelo Island. One nest of this wasp was also collected from *S. palmetto* on Patterson Island, but nests were not found on buildings in that location. No nests were found on saw palmetto, *Serenoa repens*, on either island. In contrast to our findings, Litte (1977) found nests of this wasp almost exclusively on the leaves of *Serenoa repens.* Nests were found on cabbage palm on an island in a man-made lake near Orlando, Fla., and a single nest was found on the leaf of a plant in the genus *Heliconia* (Musaceae) at that location. Bequaert (1933) mentioned a nest found in Cuba that was built on Spanish moss (*Tillandsia,* Bromeliaceae) about six feet above the ground at the periphery of a swampy margin of a stream.

Sabal palmetto (Fig. 3), most abundant on the south end of Sapelo Island, appears ideal for a nesting site because of the way in which mature leaves hang in a horizontal plane, each leaf offering a pair of nesting sites, one on each side of the midrib. *Serenoa repens,* on the other hand, has leaves that extend upward from the ground in a more-or-less vertical plane (Fig. 4). Such leaves offer very little protection from both weather and birds.

Reproductive Potential

Based on information from 10 nests, a single egg layer was apparently on each nest during the June 9–12 observation period (Table 1). This is based entirely on ovary size. Although escaping females were lost, the most gravid females of other polistine species (Hermann, unpublished) usually remain on the nest when provoked while less gravid females depart. Therefore, it is our opinion that each nest had a single egg layer. Only in one case (Nest #4) a second female on the nest had other than small, non-reproductive ovaries, and they were developed but not large.

At least half of the nests found at Sapelo Island, and probably more, were in the predaughter (= preemergence) phase. Litte (1977) also found her nests at this stage with a single egg layer. Females other than the gravid queen on nest #4 in which there were no pupae are considered to be cofoundresses. This supports the pleometrotic status of this subspecies as found earlier by Litte (1977). Our data (Table I) do no show a significant difference in wing length between the queens and non-queens (X^2 0.5 (1) = 3.841).

Predation and Potential Predators

A high degree of predation by birds of wasp nest immatures was apparent on Sapelo Island. Although bird species were not identified in this location, nests were often found shredded and abandoned, a condition characteristic of bird damage. Numbers of damaged nests were not recorded. Jeanne (1975), Richards and Richards (1951), and Turillazzi (1984) have stated that birds and ants are the most important predators of social wasps in general. Birds apparently are the most significant predators in temperate zones (Jeanne, 1975). Jeanne (1970) reported predation on *Mischocyttarus* by bats.

Litte (1977) reported seeing blue jays attacking nests of *M. m. cubicola* in south Florida and she listed the carolina wren, scrub jays, common yellowthroat, cardinal, thrashers, mockingbird and

Figures 3 and 4. Plants found to be nesting sites for *M. m. cubicola* by us and by Litte (1977). **3,** *Sabal palmetto,* showing draping nature of the leaves, making it an ideal site for nesting wasps. **4,** *Serenoa repens,* showing the nature of growth so that leaves do not drape, making them a poor site for nests.

robin as potential vertebrate predators. She also pointed out that scrub jays and red headed woodpeckers are known predators of *Polistes* adults. Invertebrate predators of wasp immatures were *Dorymyrmex flavopectus, Crematogaster ashmeadi, Pheidole floridana, Camponotus floridanus,* and *Monomorium floricola* (Formicidae). Spiders were found to catch and feed on wasp adults. Starr (1981) reported blue jays and summer tanagers as possible polistine predators. Litte (1977) found that defense against vertebrate attack was ineffective, while defense against ants was effective in most cases. Polistine wasps are apparently free of most terrestrial predators while some vespines are heavily preyed upon by them (Preiss, 1967).

Details of Nest Structure and Architectural Defense

Of the ten nests that were collected between June 9 and June 12, 1983 (Table I), six had 15 cells or more. The average number of cells was 13.90 (SD = 8.41). Although there is no information about colony growth rate at this time, it appears that most nest initiation occurred in May. Data collected from nests 1, 3, 5 and 7 (Table I) with less than 10 cells imply that either: 1) they were reinitiated after predation or 2) they were late initiators. Further study on these possibilities may give us a better understanding of the selection forces acting upon developing colonies. Most nests in June collections had a single female that dominated the face of the nest while other adult nest occupants spent much of their time on the

Table I. Nest structure, nest inhabitants and reproductive condition of females of *Mischocyttarus m. cubicola* at Sapelo Island, June 9–12, 1983.

Nest #	# of Cells (1)	Total # of adult females	Eggs	Larvae	Pupae	Female	Ovaries	Wing length (mm)
1	4	1	4	0	0	1	4LO	10.5
2	15	3	4	11	0	1	NWD	9.5
						2	NWD	9.3
						3	6LO	10
3	8	2 (1AL)	5	0	0	1	4LO	9.9
4	19	3 (1AL)	13	5	1	1	6LO	10
						2	2DO	9.8
5	8	1	4	4	0	1	3LO	10.75
6	17	3+(2AL)	4	9	4	1	NWD	10
7	3	1	1	0	0	1	5LO	9.2
8	18	4 (3AL)	7	10	1	1	4LO	9
9	31	5 (2AL)	5	9	4	–	NA	–
10	16	3	3	10	2	1	6LO	11.25
						2	NWD	9.8
						3	NWD	9.7

*Queen remained on nest during provocation 80% of time. AL, Adults lost. DO, Developing oocytes. LO, Large oocytes. NA, Information on ovaries not available; adults and nest dissected in field. NWD, Not well developed. (1) Mean number of cells = 13.90, SD = 8.41. Correlation between number of females and number of cells = 0.95, $p < 0.001$. Large oocytes are those belonging to females capable of immediate egg deposition. Females with developing oocytes are not egg laying, but there is some obvious potential for future egg laying. Females with undeveloped oocytes are non-layers with no potential for egg laying in the foreseeable future.

back of the nest. There is a significant positive correlation ($r = 0.095$, $p < 0.001$) between the number of females and the number of cells in a nest (Table I).

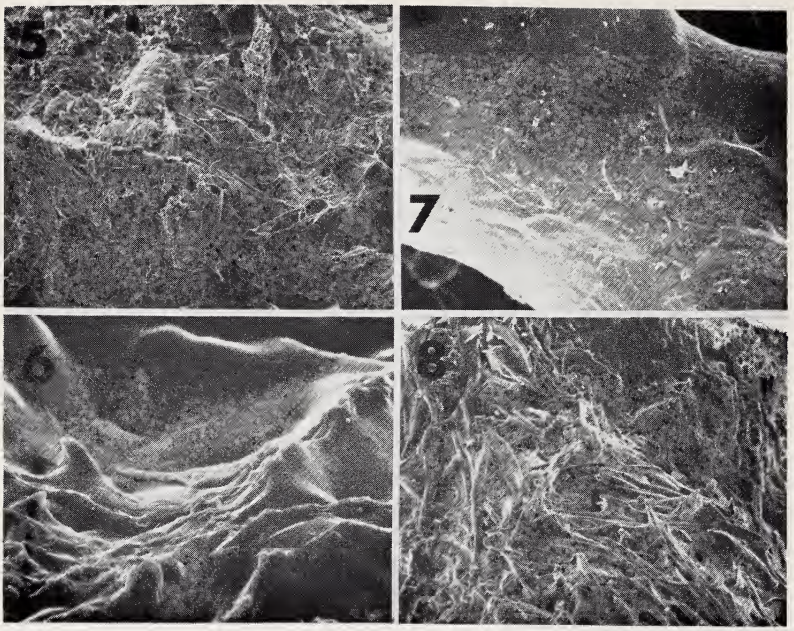
Small nests that were relatively new were light gray in color, while larger nests were often a darker, brownish color. The walls of small, young nests were translucent and the outline of a larva could be seen inside. In addition, the paper was loosely made (Fig. 8) so that occasional holes existed in the cell walls. The loose appearance and light color of the paper indicated that very little if any head secretions were added other than what was necessary to adhere the layers together. Also, very little mandibular working of the paper was done by the wasps at this time. Both paper darkening and smoothing (Figs. 6 and 7) appear to commence between the 4–5 cell stage and the time of capping.

Cell cap darkening following spinning is done by adults. Freshly spun caps were whitish while those of older pupae had brownish colored wood particles adhering to them (Fig. 5). Darkening of the caps and the addition of wood particles blended the caps with the rest of the nest, making them cryptic. This is a primary defense (Edmunds, 1974).

Another primary defense is seen in the way in which most of the nests hang on their pedicels. Some are elongate, pendulous (Fig. 1), others more round in appearance (Fig. 2). Irrespective of shape, all were constructed with the nest back away from the direction of provocation. This is most apparent on nests constructed on buildings. This allows adults to retreat from provocation rather than defend.

Nests on *Sabal palmetto* often were horizontally elongate, following the available space on the underside of the leaf. Most successful nests were constructed under leaves that had additional folds which allowed further protection from birds. Nests found in bell-like wind chimes in Haines City, Florida, were exceptionally well protected. The bells, in effect, were analogous to the bag-like (calyptodomous) nests of arboreal vespines. Predation on these nests by birds would be difficult.

Similar and other forms of architectural defense have been reported from other social hymenopterous species by numerous individuals and has been reviewed by Hermann and Blum (1981).



Figures 5–8. Scanning electron micrographs of paper from nests of *M. m. cubicola*. **5**, Cap on cell of a late pupa (nest #9, June collection, 31 cells), showing wood and other debris deposited by adult wasps, thus giving the cap a cryptic appearance (50X). **6**, Paper on outside of same nest, showing its non-woody, well-worked surface (500X). **7**, Pedicel of same nest, showing extremely smooth texture (100X). **8**, Pedicel of smaller, newer nest (nest #1, June collection, 44 cells), showing loose nature of woody constituents (100X).

Defensive Behavior other than Architectural

Young Colonies

Attack behavior as studied by numerous individuals and reviewed by Hermann and Blum (1981) appeared to be non-existent in this species during early colony life. However, a pseudoattack was elicited from wasps upon strong provocation. Strong provocation was carried out by tapping on the leaf upon which the nest was built or by actually touching the nest. Pseudoattack is defined as adult flight from the nest in the direction of the intruder. This differs from escape in which flight is not directed toward the intruder. Pseudoattack is readily demonstrated in other local polistines, e.g.,

Polistes annularis (Linnaeus) and *P. exclamans* (unpublished). We would classify pseudoattack as a very strong warning behavior. Pseudoattack was best demonstrated by *M. m. cubicola* in more mature colonies (found in August on Sapelo Island), while escape was more prevalent in younger colonies.

Other warning behaviors are as follows, some of which have been described by Jeanne (1972), Litte (1977, 1979), Starr (1981) and Windsor (1972) for this and other species of *Mischocyttarus.*

Defensive Posture—antennae forward, wings raised, body lifted and mandibles sometimes spread. Strong provocation was necessary to elicit this combination of behaviors in young nests. Litte (1979) reported that *M. flavitarsis* males and females both assume a defensive posture when disturbed.

Increased Movement on the Nest—increased movement gives the nest an agitated appearance. Increased provocation elicits increased movement by adult wasps and apparently lowers the threshhold for attack.

Wing Raising—generally with approximately an angle of 57° – 107° between wings ($\bar{X}$ = 84.6, SD = 13.7), and a mean angle of 38° above the horizontal plane of the body. While wing raising is one of the first warning behaviors elicited in most polistines (Hermann and Blum, 1981; Starr, 1981; West Eberhard, 1969), most females of *M. m. cubicola* on young nests did not raise their wings unless they were strongly provoked. Wing raising also has been reported for *M. drewseni* by Jeanne (1972) and for *M. m. cubicola* by Starr (1981). Raised wings appear to have two separate positions, a smaller angle of separation (approximately 60°) for wasps that are weakly provoked and a greater angle of separation (approximately 90–100°) for wasps that are strongly provoked. However, there is considerable overlap in these two positions.

Wing Buzzing—a prolonged wing movement, not generally demonstrated in early colonies except under strong provocation. Wing buzzing was demonstrated by *M. flavitarsis* (Litte, 1979), but adults did not attack in the pre-emergence phase. Attack was prevalent following wing buzzing in the post-emergence phase, however.

Wing fluttering—sporadic rapid flapping of wings, of a much shorter duration than buzzing. Strong provocation was necessary to elicit this behavior in young nests. Wing fluttering frequencies may be found in Table III.

Forward Jerking and Mandibular Pecking—a rapid movement forward and a biting at the object of intrusion. Pecking was also demonstrated in the absence of forward jerking. Although pecking behavior was easily elicited in a young colony, it appeared to be demonstrated in such cases almost entirely by the queen. Pecking is a behavior commonly used by adult females toward small hymenopterous parasitoid intruders. In *P. annularis,* forward jerking and pecking have been observed by us to chase and/or discard intruding ants from the nest. We witnessed such behavior in older colonies observed in August, 1983.

Backward Jerking—best demonstrated under strong provocation.

Abdominal Pumping—although abdominal pumping, a rhythymic extension and retraction of the gaster, is seen as normal behavior in all vespids, it appears to be exaggerated during provocation.

Abdominal twisting—this behavior was not evident on a young nest except under very strong provocation. However, when strongly provoked, most females of a young nest demonstrated this behavior as well as exaggerated abdominal pumping.

Movement to back of nest (retreat)—a behavior that was demonstrated upon continuous provocation. Even females that demonstrate warning behaviors move to the back of the nest upon continuous provocation.

Escape—this is readily demonstrated in young colonies under provocation. In fact, it is difficult to elicit defensive behaviors in young colonies and collect all of the adults because of their readiness to escape. Nest departure by adults of more mature colonies is expressed more as pseudoattack in which case adults return to the nest after a short erratic flight. Adults in escape flights do not return for a longer period of time.

Leg waving—this behavior was demonstrated on occasion in young colonies and readily in mature ones. Although females of young colonies are reluctant to leg wave unless strongly provoked, this behavior was less difficult to elicit in a young colony than were some of the other behaviors. Leg waving frequencies may be found in Table III.

None of the behaviors appeared to be demonstrated in a particular sequence, and many of the behaviors were demonstrated by some individuals and not by others. Escape and retreat were the most dependable behaviors in young (preemergence) colonies.

Escape and pseudoattack also occur in colonies of *P. annularis, P. exclamans* and *P. fuscatus* during the preemergence period (unpublished).

Mature Colonies

A mature colony is defined here as one in which daughters have emerged (post-emergence colony), and defensive behaviors are readily expressed, many of them requiring little provocation. Although there is very little difference in nest size between nest 9 of Table I (June collection) and nest 1 of Table II (August collection), defensive behavior in August was considerably more evident. The mean number of cells of the 4 nests collected in August (Table II) was 72.5 (SD = 46.3). Few males were found to have emerged (nests 2, 4, Table II). By comparing the colonies in June and August, we noticed that not only the colony structure changes significantly but the defensive behaviors demonstrated by colony members are also quite different. The change in defensive behaviors could be: 1) a seasonal, physiological change in adults, or 2) related to investment, such as higher total number of immatures, more older larvae and pupae, and more nesting material.

There was an apparent synchrony of movement among warning females toward a moving intruder, due in part to a periodic hooking together of their tarsi and legs. This behavior is difficult to describe and would have gone unnoticed had it not been recorded on video tape and played back at a slower speed.

A sequence of wing raising, leg waving and wing fluttering was readily apparent. Under strong provocation, wing fluttering, leg waving and exaggerated abdominal pumping were demonstrated simultaneously. The frequency of movement in leg waving was

Table II. Nest structure and inhabitants of nests of *Mischocyttarus m. cubicola* at Sapelo Island, Georgia, and Haines City, Florida, August 5–8, 23–30, 1983.

		Adults				
Nest #	# of Cells	Males	Females	Eggs	Larvae	Pupae
1(HC)	40	0	14	8	22	10
2(HC)	42	1	15	8	13	14
3(HC)	56	0	7	23	21	1
4(S)	152	3	27	16	60	38

HC, Haines City, Florida; S, Sapelo Island, Georgia. Mean number of cells = 72.5 (SD = 46.3).

Table III. Statistical Analysis of Frequencies of Readily Expressed Warning Behaviors in Colonies of *M. m. cubicola* (1)

Exp. #	Leg Waving Movements/Sec.	Wing Fluttering Beats/Sec.	Pseudoattack Flight Time in Sec.
1	8.3	5.6	2.7
2	9.1	6.3	3.3
3	7.7	6.7	1.6
4	9.1	6.3	1.6
5	9.1	5.3	5.8
6	7.1	7.7	3.7
7	7.7	5.3	2.8
8	9.1	5.6	3.7
9	7.1	6.3	9.0
10	7.7	6.7	1.6
X, SD, CV	$\bar{X}$ = 8.2 SD = .801 CV = 0.64	$\bar{X}$ = 6.18 SD = .72 CV = .51	$\bar{X}$ = 4.18 SD = 2.5 CV = 0.60

(1) Behaviors were recorded from different females.

7.1–9.1/second ($\bar{X}$ = 8.2, SD = .801, CV = .64) (Table III). The frequency of wing fluttering was 5.3–7.7/second ($\bar{X}$ = 6.2, SD = .72, CV = .51). We found no correlation (r = .07) between movement frequencies of leg waving and wing fluttering in different females (Table III). It appeared to us that a threshold had to be reached before leg waving or wing fluttering would come about, and once this threshold was reached, the duration of each behavior was dependent upon the degree of continued stimulus. However, very little variation appeared to exist in the frequencies of these behaviors in relation to the excitedness of the colony (Table III).

Pseudoattack by multiple females was easily elicited. Yet, attempts at stinging were relatively rare. Departing females flew in the direction of intrusion but most often culminated their pseudoattack with an erratic, vertically undulating flight in their return to the nest. In recording the duration of 10 randomly selected pseudoattack flights, each flight usually lasted only 1.6–9.0 seconds ($\bar{X}$ = 4.2, SD = 2.5, CV = 0.60) (Table III).

Behavior after returning to the nest often involved rapid walking on the nest face in apparent examination of the nest surface and its coinhabitants. The checking of cells and cell contents was not as

apparent as has been reported by Starr (1981) for some other polistine species. At times, females would spin in place on the nest immediately upon returning from a pseudoattack flight. Spinning is described as a rapid turning of the body throughout a small radius of movement. Also, post-attack grooming is sometimes evident.

Nests 1–3 from Haines City, Florida, reacted to provocation much like nest 4 (Table II), even through there was a considerable difference in nest size. One apparent behavioral difference existed. Nests from Haines City were adjacent to one another in metal and ceramic bell-like wind chimes. When strongly provoked, adults that left the nest in pseudoattack at times returned to a neighboring nest rather than to their own and rapidly moved around the nest face. Observing this indicates to us that possibly the three nests were initiated by siblings. We have observed similar behavior in *Polistes annularis.* Comparisons between June and August nests point out that defensive behavioral changes occur in *M. m. cubicola* as a function of time. This is also true for *P. annularis, P. fuscatus* and *P. exclamans* (unpublished) and appears to be widely recognized for other vespid species (Hermann and Blum, 1981). The major differences occur in the defensive attitude of eusocial wasps between the pre- and post-emergence periods.

Summary

Mischocyttarus mexicanus cubicola on Sapelo Island, Georgia, nests on buildings, other man-made structures and on the underside of leaves of the Cabbage Palm, *Sabal palmetto.* Although defensive behaviors expressed in young colonies at first appear to be poorly demonstrated in this subspecies, they include nest architecture and, under strong provocation, pseudoattack and subsequent erratic flight, general nest excitability, defensive posture, wing raising, wing buzzing, wing fluttering, forward jerking, mandibular pecking, backward jerking, abdominal pumping, abdominal twisting, retreat and escape. None of the warning behaviors were demonstrated in young colonies in a consistent manner or in a particular sequence. The most consistent behaviors in young colonies were retreat and escape, whereas in mature colonies all of the warning behaviors recorded for young colonies were expressed readily and in a predictable sequence.

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REVISION OF THE *MILVINA* GROUP OF THE WOLF SPIDER GENUS *PARDOSA* (ARANEAE: LYCOSIDAE)[1]

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Introduction

The genus *Pardosa* C. L. Koch is a large and widespread group of wolf spiders. Several species groups have been recognized in North America (Lowrie and Dondale 1981). The objective of the present paper is to define and revise the *milvina* group.

The *milvina* group of the genus *Pardosa* consists of 18 American species of wolf spiders. The greatest concentration of species seems to be in the southeastern United States and Mexico. Only *P. milvina* (Hentz), *P. saxatilis* (Hentz), and *P. littoralis* Banks range northward as far as Canada, and only *P. portoricensis* Banks, *P. hamifera* F. Pickard-Cambridge, and *P. littoralis* have been found in the West Indies. *P. fastosa* (Keyserling) extends into South America as far as Ecuador. None are found on the U.S. Pacific coast or in the U.S. Rocky Mountains, and few specimens are recorded from the Great Plains.

Terminology for anatomical parts is defined by Dondale and Redner (1978) and by Figures 2–7 and 41–45 here. Measurements are given as the mean and standard deviation for 10 to 20 specimens or as the range for fewer.

Relationships

The external genitalia, in our opinion, provide the best indicators of relationships within the *milvina* group. The inferred relationships among the species are shown in Figure 1.

Females of all species in the group have the lateral margins of the median septum raised and thickened at the site of the copulatory openings (character 1, Fig. 1; Fig. 45). This modification appears to enlarge the openings and to reinforce the margins, and we speculate

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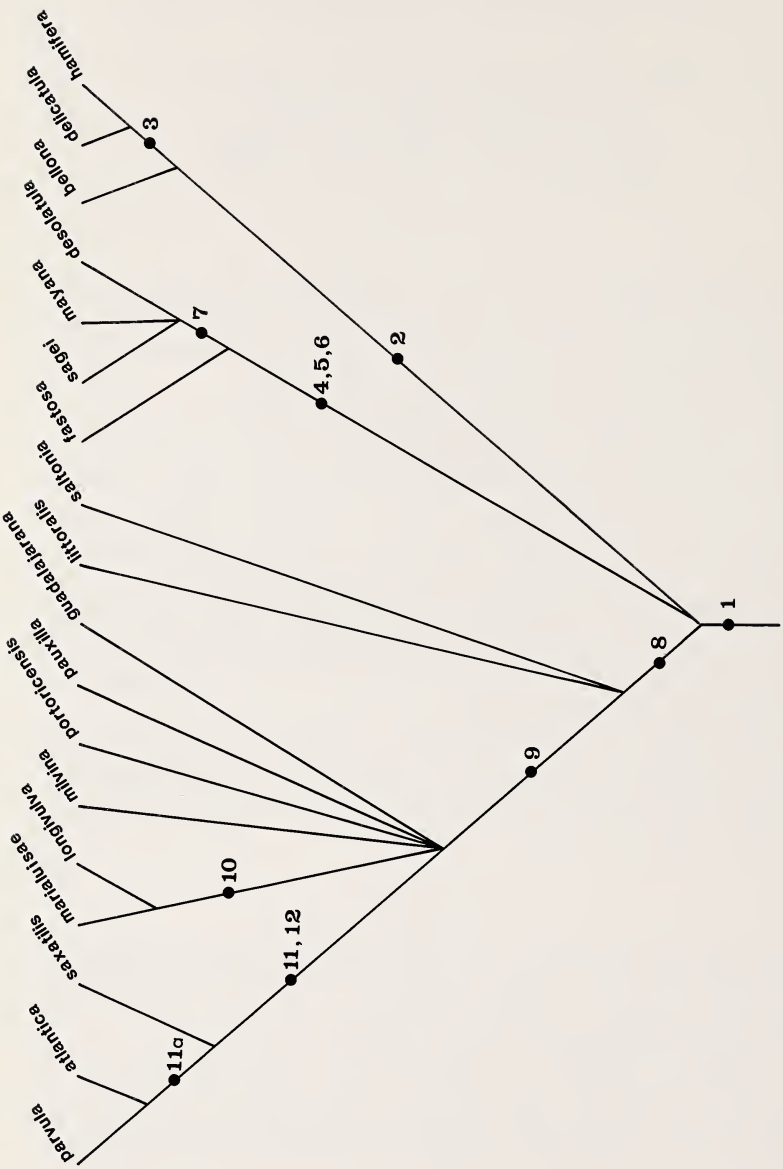


Fig. 1. Cladogram of the *milvina* group. See text for definition of the numbered components.

that each opening may accommodate not only the embolus, which is a slender shaft, but the enlarged, sclerotized tip of the conductor as well. The condition is not found elsewhere in *Pardosa* except in two species of the Old World *wagleri* group, which have a quite different kind of median septum, hood, and copulatory tubes. We infer the condition found in the *milvina* group to be apomorphic, and the absence of the condition to be plesiomorphic.

The base of the median septum is more or less rectangular in females of certain species of the group (character 4, Fig. 1; Fig. 50). This condition is unique among the species of *Pardosa,* and is inferred to be apomorphic. The plesiomorphic state is a triangular base. Also, a strongly tapered anterior part of the septum (character 9, Fig. 1; Fig. 65), in combination with a single hood cavity, is inferred to be apomorphic and a broader anterior part to be plesiomorphic.

The epigynal hood may extend posteriad at the sides, thus defining a raised, tapered, median area (character 12, Fig. 1; Fig. 58). This condition, found only in specimens of the *saxatilis* complex, is inferred to be apomorphic. The simpler, lobed hood found in the other members of the *milvina* group is inferred to be plesiomorphic.

The median apophysis, which is believed to assist indirectly in aligning the embolus tip with the copulatory opening, may be unusually short and blunt (character 2, Fig. 1; Fig. 3), with its basal process located at midlength on the apophysis (character 5, Fig. 1; Fig. 8) and having its mesal margin thickened (character 7, Fig. 1; Fig. 8). These states are inferred to be apomorphic and the more slender, elongate apophysis, with the basal process located at the base and with the mesal margin not thickened, to be plesiomorphic.

The conductor in the *milvina* group is a stout rod, lying transversely in the groove between the apical division of the genital bulb and the tegulum. In the unexpanded bulb, only its tip is visible (Fig. 3), but it becomes fully exposed by dissection (Fig. 6). The apomorphic states of this character are inferred to be "angulate or pointed on basal margin" (character 3, Fig. 1; Fig. 6), "fluted at tip" (character 6, Fig. 1; Fig. 11), "possession of dark, shiny knob near tip" (character 8, Fig. 1; Fig. 21), and "knob excavated" (character 10, Fig. 1; Figs. 38, 40, arrows). The plesiomorphic states are inferred to be "straight basal margin", "thick tip", "knob lacking", and "knob not excavated".

Certain segments of the male palpus may be covered dorsally with reflective white setae (characters 11, 11a, Fig. 1; Figs. 16–18).These setae probably serve as a visual cue to the female during male courtship, and their presence is believed to be apomorphic. In *saxatilis,* only the patella bears such a covering; in *atlantica,* both patella and tibia are covered, and in *parvula,* both segments plus the basal half of the cymbium are covered. Males of only the remotely related *P. tesquorum* (Odenwall) have a similar covering on the palpal patella. We infer that the presence of this covering in the *milvina* group is apomorphic, and that the plesiomorphic state of the character is the involvement of a single segment.

Unidentified Species

A name associated in the past with the *milvina* group, namely, *Lycosa canadensis* Blackwall, 1871, treated as a junior synonym of *P. milvina* by Chamberlin (1908), could not be identified by us, and is treated here as *nomen dubium.* The holotype of *canadensis* was an unidentifiable juvenile and is no longer in existence. *Pardosa accurata* Becker, 1886, described from "Mexico", has been identified as an unknown species of *Lycosa, s.l.,* through examination of the holotype by us; the type is a juvenile specimen deposited in the Institut Royal des Sciences Naturelles de Belgique.

Description

Total length 3.00 to 7.50 mm. Carapace smoothly convex at sides, vertical anteriorly at sides, approximately uniform in height between dorsal groove and posterior row of eyes, covered sparsely with short setae; eye area black, often iridescent; anterior row of eyes somewhat procurved, distinctly shorter than middle row, with median eyes equal in size to lateral eyes or somewhat larger and located slightly closer to laterals than to each other. Legs moderately long and strong, with thin scopulae and sparse setae; femur I with 3 dorsal macrosetae, 2 prolaterals (near tip), 2 or 3 retrolaterals; tibia I with 2 slender bristlelike dorsals, 2 prolaterals, 2 retrolaterals, 3 pairs of ventrals; basitarsus I with 1 bristlelike dorsal, 3 prolaterals, 2 or 3 retrolaterals, 3 paired and 1 unpaired ventral; trochanters with deep notch distally at tip. Abdomen ovoid, covered with dense, short setae and with cluster of longer, erect setae at anterior end.

Male palpus usually black and contrasting with pale areas on legs and carapace, often with fringes of black setae at sides of segments; palea (Fig. 6) projecting liplike at tip of genital bulb, giving rise prolaterally to slender, rather short, slightly curved embolus and giving rise basally to elongate, stout conductor that lies largely hidden between base of palea and tegulum; terminal apophysis toothlike or bladelike, located retrolaterodistally (Fig. 6); median apophysis short, straight or somewhat curved, with strong basal process (Fig. 3).

Epigynum (Fig. 41) rather long (often longer than twice maximum width of median septum), with median septum broad posteriorly and slender or evanescent anteriorly; hood small, distinct, with single cavity; copulatory openings with margins raised and thickened. Copulatory tubes (Fig. 44) short, angulate or somewhat curved, with swelling on ventral or lateral side; spermathecae small, bulbous.

KEY TO MALES OF THE *MILVINA* GROUP

1. Distal process of median apophysis short, broad, lacking hook at tip (Fig. 3) 2
1′. Distal process of median apophysis elongate, usually hooked at tip (as in Fig. 9, arrow) 4
2(1). Terminal apophysis broad (ventral view, Figs. 2, arrow, 5); conductor smoothly curved on basal margin (Fig. 5) ..... *bellona* Banks
2′. Terminal apophysis more slender (ventral view, Figs. 6, 7); conductor angular or pointed on basal margin (Figs. 6, 7, arrows) 3
3(2′). Conductor with hooked point on basal margin (Fig. 6); embolus bent near tip (Fig. 6) ..... *delicatula* Gertsch and Wallace
3′. Conductor with angulate basal margin (Fig. 7); embolus gently curved at tip (Fig. 7) ..... *hamifera* F. Pickard-Cambridge
4(1′). Median apophysis with basal process small, located about midlength of apophysis (Fig. 8); conductor thin, fluted at tip, lacking knoblike process at tip (Fig. 11) 5
4′. Median apophysis with basal process located at base of apophysis or, if located at middle then large (Figs. 19, 24);

conductor thickened at tip, bearing dark, shiny, knoblike process near tip (as in Figs. 21, 26, 38) 8

5(4). Median apophysis with distal process straight at tip (Fig. 8, arrow) ..... *sagei* Gertsch and Wallace

5′. Median apophysis with distal process hooked at tip (as in Figs. 9, 10, 14) 6

6(5′). Terminal apophysis separated from mesal swelling by acute angle (Fig. 12); median apophysis with distal process strongly hooked (Fig. 9, arrow) .... *fastosa* (Keyserling)

6′. Terminal apophysis separated from mesal swelling by broad curve (Fig. 13, arrow); median apophysis with distal process weakly hooked (Fig. 10) 7

7(6′). Median apophysis with marginal swelling broad (Fig. 10, arrow) ..... *desolatula* Gertsch and Davis

7′. Median apophysis with marginal swelling narrow (Fig. 14, arrow) ..... *mayana* sp.n.

8(4′). Patella (and sometimes additional segments) of palpus covered dorsally with reflective white setae (most noticeable in living or dried specimens) (Figs. 16–18); conductor sinuous along basal margin (Fig. 21, arrows) 9

8′. Patella of palpus covered dorsally with dark setae (though few reflective white setae may be present); conductor with single curve along basal margin (as in Figs. 25, 38)... 11

9(8). Tibia (as well as patella, and sometimes basal half of cymbium) covered dorsally with reflective white setae (Figs. 17, 18) 10

9′. Tibia of palpus covered with dark setae (Fig. 16) .... *saxatilis* (Hentz)

10(9). Basal half of cymbium (except narrow band at basal margin) covered dorsally with dark setae (Fig. 17).... .....*atlantica* Emerton

10′. Basal half of cymbium covered with reflective white setae (Fig. 18) .....*parvula* Banks

11(8′). Terminal apophysis large, extending basad to or beyond tip of embolus (Figs. 22, arrow, 25) .... *littoralis* Banks

11′. Terminal apophysis smaller, extending only short distance basad (as in Figs. 24, 35, 42) 12

12(11′). Terminal apophysis arched retrolaterally (Figs. 23, arrow, 26); median apophysis small, occupying about one-third length of genital bulb (Fig. 23) ..... *saltonia* sp.n.

12′. Terminal apophysis arched mesally, or not arched (Figs. 27, 34, 40); median apophysis larger, occupying distinctly more than one-third of genital bulb (Figs. 24, 31, 42). 13

13(12′). Terminal apophysis with mesal swelling toothlike (Fig. 27, arrow); median apophysis thick throughout most of its length, with basal process swollen (Fig. 24) .... *pauxilla* Montgomery

13′. Terminal apophysis with mesal swelling not toothlike, i.e., lacking sharp point (Fig. 34); median apophysis slender at middle (Figs. 28, 37) 14

14(13′). Median apophysis with distal process expanded (ventral view, Fig. 28, arrow). Dorsum of abdomen with pale median band flanked by paired distinct, dark, longitudinal bands ..... *portoricensis* Banks

14′. Median apophysis with distal process more slender (Figs. 31, 37, 42). Dorsum of abdomen dark or mottled, or, if pale mesally then lacking paired dark longitudinal bands 15

15(14′). Terminal apophysis broad, blunt (Fig. 30, arrow). Species occurring only north of Tropic of Cancer (Map 5) ... . *milvina* (Hentz)

15′. Terminal apophysis more slender, pointed (Figs. 33, 36, 39). Species occurring only south of Tropic of Cancer (Map 6) 16

16(15′). Median apophysis abruptly angled on mesal margin (Fig. 35, arrow). Carapace width less than 1.35 mm. Dorsum of abdomen with median band of reflective white setae .. .. *guadalajarana* sp.n.

16′. Median apophysis curved on mesal margin (Figs. 37, 42). Carapace width greater than 1.35 mm. Dorsum of abdomen lacking median band of reflective white setae 17

17(16′). Terminal apophysis rather long (Fig. 36). Tibia and basitarsus I with fringe of long, erect setae along prolateral and retrolateral surfaces. Carapace with black lateral margins ..... *longivulva* F. Pickard-Cambridge

17′. Terminal apophysis shorter (Fig. 39). Tibia and basitarsus I lacking fringe. Carapace usually with pale lateral margins ..... *marialuisae* sp.n.

KEY TO FEMALES OF THE *MILVINA* GROUP OCCURRING IN EASTERN CANADA AND UNITED STATES

1. Median septum extending anteriad nearly to level of hood (Figs. 46, 60, 65) 2
1′. Median septum extending anteriad one-half length of epigynum or less (Figs. 58, 70) 4
2(1). Median septum broad anteriorly (Fig. 60, arrow) ..... *littoralis* Banks
2′. Median septum distinctly tapered anteriorly (Figs. 46, 65) 3
3(2′). Median septum with expanded posterior part concave at lateral margins (Fig. 65, arrow) *pauxilla* Montgomery
3′. Median septum with expanded posterior part convex at lateral margins (Fig. 46, upper arrow) ..... *delicatula* Gertsch and Wallace
4(1′). Hood continuing posteriad at sides where it defines a raised, tapered median area (Fig. 58, arrows) 5
4′. Hood continuing posteriad at sides where it defines a depressed, non-tapered area (Fig. 70, arrow) ..... *milvina* (Hentz)
5(4). Species restricted to Great Lakes-St. Lawrence region and southward in Appalachian Mountains (Map 3) ..... *saxatilis* (Hentz)
5′. Species restricted to southeastern coastal plain (including Florida) and the Mississippi basin (Map 3) 6
6(5′). Species restricted to Florida and eastern Gulf Coast region (Map 3) ..... *parvula* Banks
6′. Species restricted to Atlantic coast States east of the Appalachians and in the Mississippi basin (Map 3) ... *atlantica* Emerton

KEY TO FEMALES OF THE *MILVINA* GROUP OCCURRING IN SOUTHWESTERN UNITED STATES, MEXICO, AND CENTRAL AMERICA

1. Median septum with expanded posterior part approximately rectangular (Figs. 50, 52, 54, 56) .....

..... *desolatula* Gertsch and Davis, *mayana* sp.n., *sagei* Gertsch and Wallace, and *fastosa* (Keyserling)

1′. Median septum with expanded posterior part more or less triangular (Figs. 48, 62, 68) 2

2(1′). Median septum broad anteriorly, bordered by pair of ridges that extend posteriad along interior surface of septum (Figs. 41, arrow, 43, 44) ..... *bellona* Banks

2′. Median septum slender or evanescent anteriorly, lacking bordering ridges 3

3(2′). Epigynum with curved ridges posteriorly (Figs. 46, lower arrow, 48, 72, 74, 76) 4

3′. Epigynum lacking curved ridges (Fig. 62)..... .....*saltonia* sp.n.

4(3). Curved ridges concealing lateral angles of median septum (Fig. 46, lower arrow) ....*delicatula* Gertsch and Wallace

4′. Curved ridges not concealing lateral angles of median septum 5

5(4′). Epigynum short (ratio of epigynal length to greatest median septum width less than 2:1) ....*hamifera* F. Pickard-Cambridge

5′. Epigynum longer (ratio of epigynal length to greatest median septum width more than 2:1) 6

6(5′). Carapace width usually less than 1.6 mm. Retromargin of chelicera with 2 teeth ..... *guadalajarana* sp.n.

6′. Carapace width usually greater than 1.6 mm. Retromargin of chelicera with 3 teeth 7

7(6′). Copulatory tubes with small swelling at base (Fig. 75). Carapace margins dark ....*longivulva* F. Pickard-Cambridge

7′. Copulatory tubes with large swelling on lateral margins (Fig. 77, arrow). Carapace margins usually pale ....marialuisae sp.n.

KEY TO FEMALES OF THE *MILVINA* GROUP OCCURRING IN THE WEST INDIES

1. Median septum rather broad anteriorly (Fig. 60, arrow) ..... *littoralis* Banks

1′. Median septum distinctly tapered anteriorly (Figs. 48, 68) 2

2(1′). Copulatory tubes broad, and spermathecae widely separated (Fig. 49). Epigynum long (ratio of epigynal length to greatest median septum width more than 2:1) .... *hamifera* F. Pickard-Cambridge

2′. Copulatory tubes slender, and spermathecae narrowly separated (Fig. 69, arrows). Epigynum shorter (ratio of epigynal length to greatest median septum width less than 2:1) ..... *portoricensis* Banks

Pardosa bellona Banks
Figures 2, 5, 41, 43, 44; Map 1

Pardosa bellona Banks, 1898:275, Fig. 21 (pl. 16). Two male and two female syntypes from Coral de Piedras, Baja California (Eisen and Vaslit), deposited in MCZ, examined. Syntypes from San Miguel de Horcasitas, Magdalena Island, and from San José del Cabo, deposited in California Academy of Sciences, presumed destroyed. Gertsch 1934:21. Gertsch and Wallace 1935:3, Fig. 14. Roewer 1954:189. Bonnet 1958:3359.

Male. Total length 4.50 ±0.34 mm; carapace 2.28 ±0.18 mm long and 1.75 ±0.13 mm wide (20 specimens). Carapace with dark orange median and submarginal areas, and with pair of broad, dark longitudinal bands bordering pale median area; margins dark. Sternum yellow orange, sometimes with several small black spots. Chelicerae orange brown to black, pale mesally; retromargin with 3 teeth. Legs yellow orange; femur I often black basally; tibia and basitarsus I with sparse fringe of long lateral setae. Abdomen pale mesally, dark laterally; venter orange yellow. Terminal apophysis broad; median apophysis short, broad, with large basal process, lacking hook at tip of distal process (Fig. 2); conductor rounded on basal margin (Fig. 5).

Female. Total length 4.85 ±0.35 mm; carapace 2.34 ±0.17 mm long and 1.86 ±0.13 mm wide (18 specimens). General color and structure as in male but dark pigment on carapace margin may break into spots, femur I lacking dark pigment at base, and leg I lacking fringe of long lateral setae. Median septum rather broad posteriorly, little tapered anteriorly, flanked anteriorly by ridges that continue along internal surface (Fig. 41); copulatory tubes rather thick, with swelling on ventrolateral surface (Figs. 43, 44).

Diagnosis. Specimens of *P. bellona* most resemble those of *P. delicatula* and *P. hamifera,* differing by the broad terminal

apophysis, by the rounded basal margin of the conductor, and by the anteriorly broad median septum with paired ridges.

Range. Utah south to Colima, Mexico. Included, but not mapped here, are the following: Utah: Monroe Canyon, 112° 10′W, 38° 38′N. Nevada: Las Vegas. California: Seeley, 7 mi. west of El Centro; Indian Wells, Riverside Co.

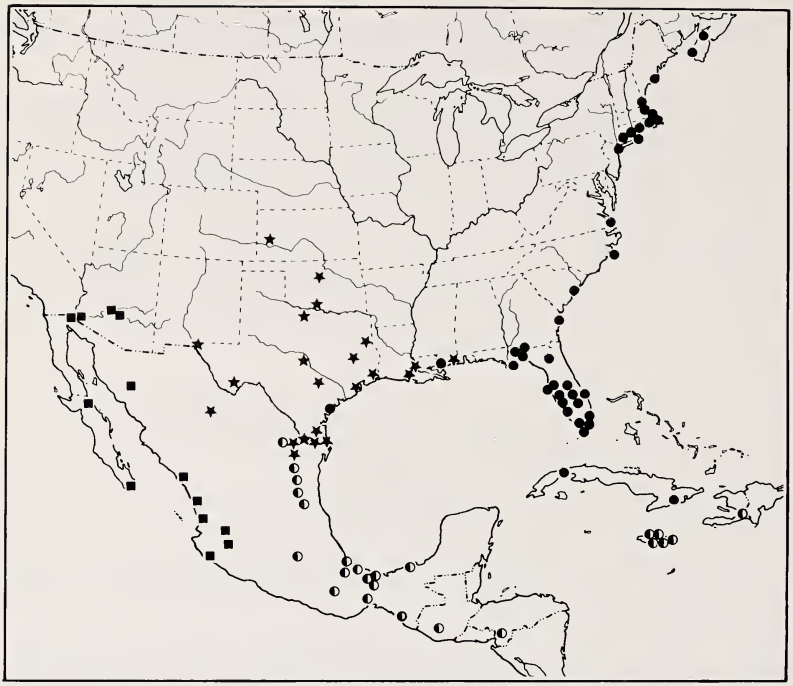
Natural History. Males have been collected in December to February, and June to September, females in January, March, June to September, and November. Females with egg sacs were collected in January, March, and May to July.

Pardosa delicatula Gertsch and Wallace
Figures 3, 6, 45–47; Map 1

Pardosa pauxilla: Montgomery 1904:268 (part, not lectotype).
Pardosa delicatula Gertsch and Wallace, 1935:4, Figs. 13, 17.
Male holotype and female allotype from Edinburg, Hidalgo Co., Texas (Stanley Mulaik), deposited in AMNH, examined. Gertsch and Davis, 1940: 5. Roewer 1954:189. Bonnet 1958:3365.

Male. Total length 4.78 ±0.32 mm; carapace 2.59 ±0.15 mm long and 1.90 ±0.14 mm wide (20 specimens). Carapace with dark orange median and submarginal areas, and with pair of dark brown longitudinal bands flanking pale median area; margins dark, pale, or marked with series of 3 or 4 dark spots. Sternum orange yellow, sometimes suffused with black or with faint, V-shaped dark mark. Chelicerae variable in color; retromargin with 3 teeth. Legs yellow orange; femur I dark prolaterally at base. Abdomen dull yellow mesally, darker laterally, sometimes black throughout; venter pale. Terminal apophysis rather slender (ventral view); median apophysis short, broad, with large basal process, lacking hook at tip of distal process (Fig. 3); conductor with sharp, hooked point on ventral surface; embolus bent near tip (Fig. 6).

Female. Total length 5.73 ±0.79; carapace 2.63 ±0.20 mm long and 2.02 ±0.23 mm wide (20 specimens). General color and structure as in male but carapace paler, usually having pale margins. Median septum strongly tapered anteriorly, lacking lateral ridges, convex along lateral margins of posterior part, partly concealed laterally by curved ridges (Fig. 46); copulatory tubes rather slender (Fig. 47).



Map 1. Collection localities for *Pardosa bellona* (squares), *P. delicatula* (stars), *P. hamifera* (half-circles), *P. littoralis* (circles).

Diagnosis. Specimens of *P. delicatula* most resemble those of *P. bellona* and *P. hamifera* but differ by the sharp, hooked point on the conductor, by the bent embolus, and by the concealment of the lateral angles of the median septum by curved ridges.

Range. Oklahoma and Mississippi south to Chihuahua and Nuevo Leon, Mexico.

Natural History. Males and females have been collected in every month except January, and females with egg sacs were taken from April to October. Common habitats are pastures and other grasslands, where they are taken in numbers by pitfall trap; one large collection was taken by sweep net in Louisiana sweet potato fields at night.

Pardosa hamifera F. Pickard-Cambridge
Figures 4, 7, 48, 49; Map 1

Pardosa hamifera F. Pickard-Cambridge, 1902:320, Fig. 4, 4a (pl. 31). Holotype male from Guatemala (Sarg), deposited in BM(NH), examined. Roewer 1954:187. Bonnet 1958:3373.

Pardosa delicata Gertsch, 1934:20. Holotype female from La Zacualpa, Chiapas, Mexico, August 1909 (A. Petrunkevitch), deposited in AMNH, examined. Allotype male and paratype female from the type locality, with same data as for holotype, not examined. Gertsch and Wallace 1935:3, Fig. 18. Roewer 1954:186. Bonnet 1958:3365. **NEW SYNONYM.**

Male. Total length 4.54 ±0.38 mm; carapace 2.36 ±0.18 mm long and 1.83 ±0.14 mm wide (20 specimens). Carapace with dark orange brown median and submarginal areas, and with dark longitudinal bands flanking median area; lateral margins usually pale. Sternum dark orange, sometimes paler or darker mesally. Chelicerae variable in color; retromargin with 3 teeth. Legs dark orange; femur I often dark at base. Abdomen black with dull yellow heart mark, or yellow brown mesally and darker laterally; venter pale, sometimes suffused with black. Terminal apophysis slender (ventral view); median apophysis short, broad, with large basal process, lacking hook at tip of distal process (Fig. 4); conductor angled on basal margin (Fig. 7).

Female. Total length 5.10 ±0.48 mm; carapace 2.45 ±0.22 mm long and 1.95 ±0.19 mm wide (20 specimens). General color and structure as in male but paler. Median septum slender anteriorly, lacking lateral ridges, concave at lateral margins of expanded posterior part (Fig. 48); copulatory tubes rather thick throughout, with ventral swelling (Fig. 49).

Diagnosis. Specimens of *P. hamifera* most resemble those of *P. bellona* and *P. delicatula* but differ in having an angular basal margin on the conductor, a gently curved embolus (as in *bellona* but not as in *delicatula*), and in having a slender anterior part and fully exposed posterior part of the median septum.

Range. Nuevo Leon south to Honduras; Jamaica, Haiti.

Natural History. Males have been collected in Feburary, March, June, and August to December, females in all months except April and September. Habitat is unrecorded.

Pardosa sagei Gertsch and Wallace
Figures 8, 11, 50, 51; Map 2

Pardosa sagei Gertsch and Wallace, 1937:1, Figs. 1,2. Holotype male and allotype female from El Volcan, Chiriqui, Panama, 26 February 1936 (W. J. Gertsch), deposited in AMNH, examined. Three paratype males and four paratype females from the type locality, with same data as holotype, deposited in MCZ, examined. Roewer 1954:188. Bonnet 1958:3420.

Male. Total length 5.00 ±0.35 mm; carapace 2.69 ±0.12 mm long and 2.40 ±0.10 mm wide (20 specimens). Carapace yellow orange mesally and submarginally, with pair of dark longitudinal bands flanking mesal area; margins dark. Sternum orange yellow, sometimes with few black spots. Chelicerae yellow orange; retromargin with 3 teeth. Legs yellow orange; tibia and basitarsus I with fringe of long, erect, lateral setae. Abdomen yellow brown mesally, darker laterally; venter pale yellow, sometimes with few small black spots. Terminal apophysis small, pointed (ventral view); median apophysis with distal process elongate and straight, with basal process small, located about midlength on apophysis (Fig. 8); conductor thin, fluted at tip, lacking knoblike process (Fig. 11).

Female. Total length 5.38 ±0.57 mm; carapace 2.63 ±0.18 mm long and 2.04 ±0.18 mm wide (20 specimens). General color and structure as in male but leg I lacking fringe of setae. Median septum with posterior part approximately rectangular (Fig. 50). Copulatory tubes rather thick, curved near middle (Fig. 51).

Diagnosis. Specimens of *P. sagei* most resemble those of *P. fastosa, P. desolatula,* and *P. mayana.* Males of *sagei* are diagnosed by the straight distal process of the median apophysis. Diagnostic characters are not available for female *sagei;* the known females were collected together with males.

Range. Panama.

Natural History. Males and females have been collected in February, March, July, and August. Egg sacs were found in July and August.

Pardosa fastosa (Keyserling)
Figures 9, 12, 52, 53; Map 2

Lycosa fastosa Keyserling, 1877:618, Figs. 5, 6 (pl. 1). Six syntype males and four syntype females from "Umgebung von St. Fé de Bogota", Bogota, Colombia

(Lindig), deposited in BM(NH), examined.

Pardosa fastosa: Petrunkevitch 1911:570. Roewer 1954:186.

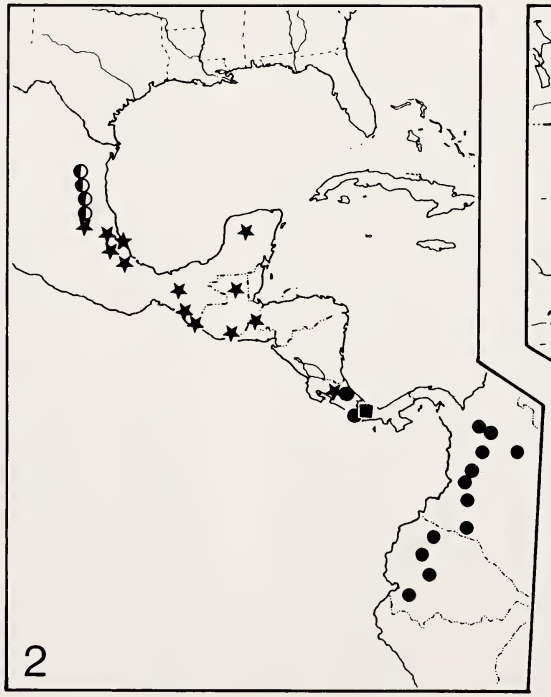
Pardosa fastuosa: Bonnet 1958:3367 (incorrect subsequent spelling).

Pardosa uncatula F. Pickard-Cambridge, 1902:319, Figs. 27, 28 (pl. 30). Lectotype male from La Palma, Costa Rica (Tristan), deposited in BM(NH), examined and here designated. Three paralectotype males and six paralectotype females from the type locality, with same data as lectotype, deposited in BM(NH) and here designated. One male and two females from original syntype series, collected at the type locality and with same data as lectotype, described herein as *P. mayana* new species. Banks 1909:219. Gertsch 1934:20 (part; proposed synonymy of *uncatula* with *pauxilla,* later disclaimed by Gertsch and Wallace (1935)). Roewer 1954:190 (part). Bonnet 1958:3427 (part). **NEW SYNONYM.**

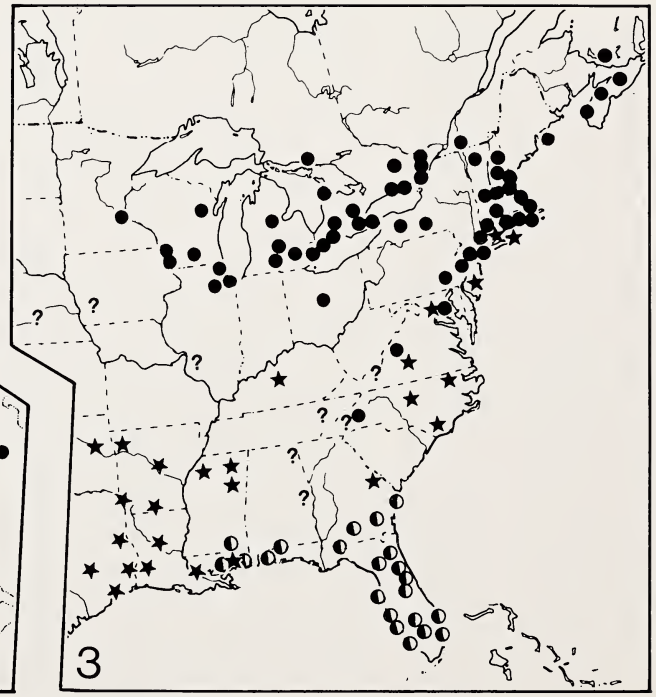
Male. Total length 5.26 ±0.39 mm; carapace 2.73 ±0.22 mm long and 2.09 ±0.17 mm wide (20 specimens). Carapace with orange yellow median and submarginal areas, and with paired dark longitudinal bands flanking median area; lateral margins dark. Sternum black, with pale mesal band anteriorly. Chelicerae dark orange, with black lines; retromargin with 3 teeth. Legs yellow orange; femora I and II dark at base; tibia and tarsus I with lateral fringe of long setae. Abdomen black, with dull yellow heart mark; venter yellow, reticulated with black. Terminal apophysis stout, toothlike, connected to mesal swelling by acute angle (ventral view); median apophysis with distal process strongly hooked at tip (Fig. 9); conductor thin, fluted at tip, lacking knoblike process at tip (Fig. 12).

Female. Total length 5.57 ±0.54 mm; carapace 2.70 ±0.23 mm long and 2.11 ±0.20 mm wide (20 specimens). General color and structure essentially as in male, but leg I lacking fringe and black pigment, and pale median area of abdominal dorsum extended posteriad as series of chevrons. Median septum with posterior part approximately rectangular (Fig. 52); copulatory tubes stout, diverging (Fig. 53).

Diagnosis. Males of *P. fastosa* most resemble those of *P. sagei, P. desolatula,* and *P. mayana,* but differ in having the terminal apophysis connected to the swelling lying mesal to that apophysis by an acute angle rather than by a curve, and by the strongly hooked tip of the median apophysis. Females of *fastosa* are anatomically indistinguishable from those of *sagei, desolatula,* and *mayana,* but most specimens examined were accompanied by males, or originated in localities from which no males of the other species were known.



Map 2. Collection localities for *Pardosa sagei* (square), *P. fastosa* (circles), *P. desolatula* (half-circles), *P. mayana* (stars).



Map 3. Collection localities for *Pardosa saxatilis* (circle), *P. atlantica* (stars), *P. parvula* (half-circles). Question marks indicate localities for females of uncertain identity; Nebraska locality was confirmed by discovery of males after the paper was submitted for publication.

Range. Costa Rica to Ecuador. The record of *uncatula* from Panama by Petrunkevitch (1925) was not confirmed. The type of *Lycosa fastosa viota* Strand, 1914, was not found.

Natural History. Males have been collected in every month except February and May, and females in every month except May. Females with egg sacs were collected in March, April, July, August, and October to December. Specimens have been recorded from 1,000 to 3,200 meters elevation.

Pardosa desolatula Gertsch and Davis
Figures 10, 13, 54, 55; Map 2

Pardosa desolatula Gertsch and Davis, 1940:5, Fig. 22. Holotype male and 1 paratype female from Ciudad Victoria, Tamaulipas, Mexico, 12 June 1936 (L. I. Davis), deposited in AMNH, examined. Allotype female from Tamazunchale, San Luis Potosi, Mexico, 25 November 1938 (A. M. and L. I. Davis), deposited in AMNH, examined. Roewer 1954:186. Vogel 1967:104.

Male. Total length 3.82–4.55 mm; carapace 2.05–2.42 mm long and 1.53–1.87 mm wide (5 specimens). Carapace with yellow orange to orange brown median and submarginal areas, and with paired dark longitudinal bands flanking pale median area; lateral margins pale to dark. Sternum yellow orange. Chelicerae orange brown to brown; retromargin with 3 teeth. Legs orange yellow; femur I dark on basal half to two-thirds. Abdomen dull yellow brown mesally, darker laterally; venter pale. Terminal apophysis connected to mesal swelling by broad curve; median apophysis with marginal swelling broad, and with distal process weakly hooked (Fig. 10); conductor thin, fluted at tip, lacking knoblike process at tip (Fig. 13).

Female. Total length 4.50 ±0.60 mm; carapace 2.17 ±0.19 mm long and 1.65 ±0.17 mm wide (10 specimens). General color and structure essentially as in male, but femur I not black. Median septum with posterior part essentially rectangular (Fig. 54); copulatory tubes stout, diverging (Fig. 55).

Diagnosis. Males of *P. desolatulata* most resemble those of *P. sagei, P. fastosa,* and *P. mayana,* but can be distinguished by the broad marginal swelling and weak hook on the median apophysis and by the broad curve by which the terminal apophysis is connected to the mesal swelling. Females are not distinguishable

anatomatically from those of *sagei, fastosa,* or *mayana,* but all of those examined were accompanied by males, or originated in localities from which no males of the other species were known.

Range. San Luis Potosi and Tamaulipas, Mexico.

Natural History. Males have been collected in March, June, and November, and females in March, April, September, and November.

Pardosa mayana sp.n.
Figures 14, 15, 56, 57; Map 2

Pardosa uncatula F. Pickard-Cambridge, 1902:319 (part, not lectotype nor paralectotypes).

Type Material. Holotype male from 2 miles north of Fortin de las Flores, 97°01'W, 13°56'N, Veracruz, Mexico, 5 August 1966 (Jean and Wilton Ivie), deposited in AMNH. Three paratypes from La Palma, Costa Rica, deposited in BM(NH). Two paratypes from Honduras and Guatemala, deposited in MCZ. Eighty-seven paratypes from Mexico, Guatemala, and Honduras, deposited in AMNH.

Male. Total length 4.47 ±0.26 mm; carapace 2.40 ±0.11 mm long and 1.84 ±0.08 mm wide (20 specimens). Carapace with yellow orange median and submarginal areas, and with paired dark longitudinal bands flanking median area; lateral margins pale or dark. Sternum yellow orange. Chelicerae yellow brown; retromargin with 3 teeth. Legs yellow orange; femur I sometimes black basally; tibiae and tarsi I with fringe of long lateral setae. Abdomen dull yellow brown mesally, darker laterally; venter pale. Terminal apophysis connected to mesal swelling by broad curve; median apophysis with narrow marginal swelling and with distal process weakly hooked (Fig. 14); conductor thin, fluted at tip, lacking knoblike process at tip (Fig. 15).

Pardosa desolatula Gertsch and Davis
Figures 10, 13, 54, 55; Map 2

Pardosa desolatula Gertsch and Davis, 1940:5, Fig. 22. Holotype male and 1 paratype female from Ciudad Victoria, Tamaulipas, Mexico, 12 June 1936 (L. I. Davis), deposited in AMNH, examined. Allotype female from Tamazunchale,

San Luis Potosi, Mexico, 25 November 1938 (A. M. and L. I. Davis), deposited in AMNH, examined. Roewer 1954:186. Vogel 1967:104.

Male. Total length 3.82–4.55 mm; carapace 2.05–2.42 mm long and 1.53–1.87 mm wide (5 specimens). Carapace with yellow orange to orange brown median and submarginal areas, and with paired dark longitudinal bands flanking pale median area; lateral margins pale to dark. Sternum yellow orange. Chelicerae orange brown to brown; retromargin with 3 teeth. Legs orange yellow; femur I dark on basal half to two-thirds. Abdomen dull yellow brown mesally, darker laterally; venter pale. Terminal apophysis connected to mesal swelling by broad curve; median apophysis with marginal swelling broad, and with distal process weakly hooked (Fig. 10); conductor thin, fluted at tip, lacking knoblike process at tip (Fig. 13).

Female. Total length 4.50 ±0.60 mm; carapace 2.17 ±0.19 mm long and 1.65 ±0.17 mm wide (10 specimens). General color and structure essentially as in male, but femur I not black. Median septum with posterior part essentially rectangular (Fig. 54); copulatory tubes stout, diverging (Fig. 55).

Diagnosis. Males of *P. desolatulata* most resemble those of *P. sagei, P. fastosa,* and *P. mayana,* but can be distinguished by the broad marginal swelling and weak hook on the median apophysis and by the broad curve by which the terminal apophysis is connected to the mesal swelling. Females are not distinguishable anatomatically from those of *sagei, fastosa,* or *mayana,* but all of those examined were accompanied by males, or originated in localities from which no males of the other species were known.

Range. San Luis Potosi and Tamaulipas, Mexico.

Natural History. Males have been collected in March, June, and November, and females in March, April, September, and November.

Pardosa mayana sp.n.
Figures 14, 15, 56, 57; Map 2

Pardosa uncatula F. Pickard-Cambridge, 1902:319 (part, not lectotype nor paralectotypes).

Type Material. Holotype male from 2 miles north of Fortin de las Flores, 97°01'W, 13°56'N, Veracruz, Mexico, 5 August 1966 (Jean

and Wilton Ivie), deposited in AMNH. Three paratypes from La Palma, Costa Rica, deposited in BM(NH). Two paratypes from Honduras and Guatemala, deposited in MCZ. Eighty-seven paratypes from Mexico, Guatemala, and Honduras, deposited in AMNH.

Male. Total length 4.47 ±0.26 mm; carapace 2.40 ±0.11 mm long and 1.84 ±0.08 mm wide (20 specimens). Carapace with yellow orange median and submarginal areas, and with paired dark longitudinal bands flanking median area; lateral margins pale or dark. Sternum yellow orange. Chelicerae yellow brown; retromargin with 3 teeth. Legs yellow orange; femur I sometimes black basally; tibiae and tarsi I with fringe of long lateral setae. Abdomen dull yellow brown mesally, darker laterally; venter pale. Terminal apophysis connected to mesal swelling by broad curve; median apophysis with narrow marginal swelling and with distal process weakly hooked (Fig. 14); conductor thin, fluted at tip, lacking knoblike process at tip (Fig. 15).
Female. Total length 4.86 ±0.53 mm; carapace 2.40 ±0.17 mm long and 1.89 ±0.15 mm wide (20 specimens). General color and structure as in male, but leg I lacking dark pigment and fringe. Median septum with posterior part approximately rectangular (Fig. 56). Copulatory tubes rather stout, diverging (Fig. 57).

Diagnosis. Males of *P. mayana* most resemble those of *P. sagei, P. fastosa,* and *P. desolatula,* but can be distinguished by the narrow marginal swelling and weakly hooked distal process on the median apophysis, and by the broad curve by which the terminal apophysis is connected to the mesal swelling. Females are not anatomically distinguishable from those of *sagei, fastosa,* and *desolatula,* but all of those examined were accompanied by males, or originated in localities from which no males of the other species were known.

Range. Hidalgo, Mexico to Costa Rica.

Natural History. Males and females have been collected in every month except November to January. Females with egg sacs were collected in March and July.

Derivation of Specific Name. The name is derived from that of the Maya Indians.

Pardosa saxatilis (Hentz)
Figures 16, 19–21, 58, 59; Map 3

Lycosa saxatilis Hentz, 1844:392, Figs. 9, 10 (pl. 18). Syntype females from "The mountains of North Alabama", August, destroyed. Hentz 1875:34, Figs. 9, 10 (pl. 4).

Lycosa minima Keyserling, 1877:614, Fig. 3 (pl. 7). Holotype male from Peoria, Illinois, deposited in BM(NH), examined. Banks 1891:193.

Pardosa albopatella Emerton, 1885:497, Fig. 2, 2*a*, 2*b* (pl. 49). Four syntype males and 1 juvenile syntype male from New Haven, Connecticut, 20 May 1884 (J. H. Emerton), deposited in MCZ, examined; syntypes from Ipswich and Roxbury, Massachusetts (May and June), not found. Banks 1892:70. Barrows 1918:314.

Pardosa annulata Banks, 1892:68, Fig. 41 (pl. 1). Two syntype females from Ithaca, New York, deposited in MCZ, examined.

Pardosa minima: Banks 1895:91. Montgomery 1902:571, Figs. 35, 36 (pl. 30); 1904:273.

Pardosa saxatilis: Chamberlin 1908:174, Figs. 1, 2 (Pl. 13). Chickering 1933:517. Comstock 1940:661, Fig. 732*d*. Kaston 1948:335, Fig. 1104 (pl. 56), 1124, 1125 (pl. 58), 1139 (pl. 59); 1978:191, Fig. 487 (part). Levi and Field 1954:456. Roewer 1954:194 (part). Bonnet 1958:3420 (part). Wolff 1981:66, Figs. 10, 18.

Pardosa platta Chamberlin and Ivie, 1942:31, Fig. 72 (pl.7). Holotype female from 10 mi. west of Grand Island, Hall Co., Nebraska, 6 June 1933 (W. Ivie), in AMNH, examined. Roewer 1954:194. Vogel 1967: 105. **NEW SYNONYM.**

Male. Total length 4.24 ±0.40 mm; carapace 2.27 ±0.18 mm long and 1.71 ±0.14 mm wide (20 specimens). Carapace (Fig. 20) with dark orange or dark yellow median and submarginal areas, and with paired dark, indistinct, longitudinal bands flanking median area; margins pale or with series of dark spots. Sternum dark orange suffused with black. Chelicerae dark brown, streaked with black; retromargin usually (about 85%) with 2 teeth, more rarely with 3. Legs orange yellow; femur I dark. Abdomen dark orange mottled with brown and black mesally, darker laterally; venter dark orange brown. Terminal apophysis small, blunt; median apophysis long, slender, curved (Fig. 19); conductor sinuous along basal margin, with dark, shiny knob near tip (Fig. 21); patella covered dorsally with reflective white setae, and remaining palpal segments dark (Fig. 16).

Female. Total length 4.48 ±0.38 mm; carapace 2.27 ±0.14 mm long and 1.75 ±0.14 mm wide (20 specimens). General color and structure as in male but pale areas on carapace more extensive and more distinct, femur I lacking dark area, rings on distal segments of legs more distinct, and retromargin of chelicera with 2 teeth in

approximately 55% of specimens. Median septum extending anteriad approximately one-half length of epigynum; hood continuing posteriad at sides where it defines a raised, tapered median area (Fig. 58); copulatory tubes short, slender, with distinct lateral swellings (Fig. 59).

Diagnosis. Specimens of *P. saxatilis* most resemble those of *P. atlantica* and *P. parvula* but differ in having the dorsal cover of reflective white setae restricted to the palpal patella. Females are not distinguishable from those of *atlantica* or *parvula* except geographically (see map 3).

Range. Nebraska and Minnesota to Nova Scotia, south to northern Alabama and North Carolina. No specimens were available from the type locality of *P. saxatilis,* i.e., northern Alabama, for this study. Thorough collecting there would help to confirm our position regarding the identity of this species.

Natural History. Males have been collected in March, May to September, and November, and females May to September. Females with egg sacs were taken in June, July, and September. The usual habitats are grassy fields or meadows but a few specimens also come from marshes, bogs, deciduous woods, or sandy beaches. Wolff (1981) gives life history and related data in Michigan.

Pardosa atlantica Emerton
Figure 7; Map 3

Pardosa sp. near *saxatilis:* Banks 1899:189.

Pardosa atlantica Emerton, 1913:258, Fig. 7, 7*a* (pl. 48). Syntype male and female from Lakehurst, New Jersey, 1 May 1912 (J. H. Emerton), deposited in MCZ, examined; three syntype males from the same locality (same data), deposited in AMNH, examined. Syntype from Fire Island beach, Long Island, New York, not found. Chamberlin and Ivie 1944:147.

Pardosa saxatilis: Gertsch 1934:22 (part). Roewer 1954:194 (part). Bonnet 1958:3420 (part).

Pardosa saxatilis var. *atlantica:* Kaston 1938:184; 1948:335. Howell and Pienkowski 1971:164.

Male. Total length 3.53 ±0.27 mm; carapace 1.89 ±0.15 mm long and 1.42 ±0.12 mm wide (20 specimens). Carapace with dark orange or dark yellow median and submarginal areas, and with paired dark, indistinct, longitudinal bands flanking median area; margins

pale or with dark spots. Sternum dark orange suffused with black. Chelicerae dark brown, streaked with black; retromargin usually (about 67%) with 3 teeth. Legs orange yellow; femur I dark basally. Abdomen dark orange mottled with brown and black mesally, darker laterally; venter dark orange brown. Terminal apophysis small, blunt; median apophysis long, slender, curved; conductor sinuous along basal margin, with dark, shiny knob near tip; patella, tibia, and small basal area of cymbium covered dorsally with reflective white setae, and remaining palpal segments dark (Fig. 17). Female. Total length 4.03 ±0.50 mm; carapace 1.94 ±0.20 mm long and 1.48 ±0.19 mm wide (20 specimens). General color and structure as in male, but pale areas on carapace more extensive and more distinct, femur I lacking dark area, dark rings on distal segments of legs more distinct, and retromargin of chelicera with 3 teeth in 75% of specimens. Median septum extending anteriad approximately one-half length of epigynum; hood continuing posteriad at sides where it defines a raised, tapered, median area; copulatory tubes short, slender, with distinct lateral swellings.

Diagnosis. Males of *P. atlantica* most resemble those of *P. saxatilis* and *P. parvula* but differ in having a dorsal cover of reflective white setae on the patella, tibia, and small basal area of the cymbium of the palpus. Females are not distinguishable from those of *saxatilis* or *parvula* except geographically (see map 3).

Range. Eastern Oklahoma and eastern Texas to Long Island, New York and Connecticut. The range may extend westward to Kansas, but the westernmost records are based on females, which we are at present unable to distinguish on anatomical characters.

Natural History. Males have been collected from February to August, and females from April to August. Females with egg sacs were collected from June to August. The few specimens for which habitat data are available were found in pine or pine-oak forests or at the edge of mixed deciduous forests. One specimen was found in a one-year abandoned field, and Howell and Pienkowski (1971) recorded the species from alfalfa at Blacksburg, Virginia. Emerton's (1913) type series was collected on "low sandy ground". Chamberlin and Ivie (1944) found *atlantica* "in company with" *parvula* (reported as *saxatilis*) near Sylvania, Georgia.

Pardosa parvula Banks
Figure 18; Map 3

Pardosa parvula Banks, 1904*b*:114, Fig. 24 (pl. 6). Holotype male from Altoona, Florida (Dobbin), deposited in MCZ, examined. Banks 1910:59.
Pardosa saxatilis: Petrunkevitch 1911:574 (part). Chamberlin and Ivie 1944:149. Muma 1973:180.

Male. Total length 3.37 ±0.21 mm; carapace 1.84 ±0.09 mm long and 1.41 ±0.08 mm wide (19 specimens). Carapace with dark orange or dark yellow median and submarginal areas, and with paired dark, longitudinal bands flanking median area; margins pale or dark. Sternum dark orange suffused with black. Chelicerae dark brown, streaked with black; retromargin with 3 teeth. Legs orange yellow; femur I dark basally. Abdomen dark orange mottled with brown and black mesally, darker laterally; venter dark orange brown. Terminal apophysis small, blunt; median apophysis long, slender, curved; conductor sinuous along basal margin, with dark, shiny knob near tip; patella, tibia, and basal half of cymbium covered dorsally with reflective white setae, and remaining palpal segments dark (Fig. 18).

Female. Total length 3.84 ±0.43 mm; carapace 1.95 ±0.15 mm long and 1.53 ±0.12 mm wide (20 specimens). General color and structure as in male but pale areas on carapace more extensive and more distinct, femur I lacking dark area, and dark rings on distal segments of legs more distinct. Median septum extending anteriad approximately one-half length of epigynum; hood continuing posteriad at sides where it defines a raised, tapered, median area; copulatory tubes short, slender, with distinct lateral swellings.

Diagnosis. Males of *P. parvula* most resemble those of *P. saxatilis* and *P. atlantica* but differ in having a dorsal cover of reflective white setae on the palpal patella, tibia, and basal half of the cymbium.Females are not distinguishable from those of *saxatilis* and *atlantica* except geographically (see map 3).

Range. Southeastern Louisiana to Florida and southern Georgia.

Natural History. Males have been collected from January to April, and in June, July, September, and October, females from January to May, and in August, October, and December. Females with egg sacs were collected in January, March, and December. The

recorded habitats are roadside grass and a mowed field, a sugar cane field, and on the ground in goldenrod and pine flat-woods. Chamberlin and Ivie (1944) found *parvula* (reported as *P. saxatilis*) "in company with" *atlantica* near Sylvania, Georgia.

Pardosa littoralis Banks
Figures 22, 25, 60, 61; Map 1

Pardosa littoralis Banks, 1896:192. Five syntype males, 2 syntype females, and 1 syntype juvenile from Mill Neck, Long Island, New York, June, deposited in MCZ, examined. Emerton 1909:207, Figs. 5, 5*a*, 5*b* (pl. 6); 1930:169.

Pardosa longispinata Tullgren, 1901:23, Fig. 13 (pl. 1). Holotype female from Lake Leonore, Orange County, Florida (E. Lonnberg), deposited in Zoological Institute, Uppsala University, not examined. Banks 1904*a*:121; 1910:59. Chamberlin 1908:209. Petrunkevitch 1911:572. Wallace 1950:77, Figs. 3, 4 (pl. 1). Roewer 1954:189. Bonnet 1958:3381. Muma 1973:180; 1975:86.

Pardosa floridana Banks, 1904*a*:136, Fig. 1 (pl. 7), Fig. 15 (pl. 8). Holotype female from Enterprise, Florida, deposited in MCZ, examined. Banks 1910:59. Gertsch 1934:21. Gertsch and Wallace 1935:5, Figs. 12, 16; 1937:3. Muma 1945:21. Kaston 1948:336, Fig. 1126 (pl. 58), Figs. 1140, 1141 (pl. 59). Bonnet 1958:3369.

Pardosa banksi Chamberlin, 1904:175. New name for *Pardosa littoralis* Banks, mistakenly believed to be preoccupied. Chamberlin 1908:182, Fig. 7 (pl. 13). Banks 1910:58. Petrunkevitch 1911:569.

Pardosa ocala Bryant, 1935:81, Fig. 12 (pl. 5). Holotype female from Hale's Siding, Alachua County, Florida, 14 October 1933 (Wallace), deposited in MCZ, examined. Paratype female from Lake County, 9 October 1933 (H. K. Wallace), not found.

Male. Total length 5.07 ±0.42 mm; carapace 2.66 ±0.19 mm long and 2.03 ±0.16 mm wide (20 specimens). Carapace with orange or yellow orange mesal and submarginal areas, and with paired dark, longitudinal bands flanking mesal area; lateral margins usually dark. Sternum orange with marginal black spots and dark mesal band or V-shaped mark, rarely entirely black. Chelicerae orange; retromargin with 3 teeth. Legs orange or yellow orange; femur I sometimes dark basally, usually more so in northern specimens. Abdomen black, sometimes with pale heart mark and series of pale spots at midline, or mottled with yellow brown; heart mark with narrow band of white setae; venter dull yellow, sometimes with small dark spots. Terminal apophysis long, stout, tapered, extending to or beyond tip of embolus; median apophysis broad at base, slender and curved at tip (Fig. 22); conductor with single curve on basal margin, directed retrolaterobasad, with dark, shiny knob near tip (Fig. 25).

Female. Total length 5.87 ±0.65 mm; carapace 2.83 ±0.32 mm long and 2.19 ±0.32 mm wide (20 specimens). General color and structure as in male but paler, with the abdominal dorsum having only scattered black spots on a yellowish background. Median septum extending anteriad nearly to level of hood, rather broad anteriorly (Fig. 60); copulatory tubes short, slender, with lateral swellings (Fig. 61).

Diagnosis. Specimens of *P. littoralis* are unique in the *milvina* group by the greatly elongated terminal apophysis and by the anteriorly broad median septum.

Range. Texas to Florida, northward near the coast to the Bay of Fundy, Nova Scotia; Cuba.

Natural History. Both sexes of *P. littoralis* have been collected in every month in the southern part of its range, and egg sacs were observed in April, June to August, and December. In general it is an inhabitant of salt marshes, though Florida records include beaches, lake shores, pine-oak forests, and swamps. One specimen was collected in a soybean field. Muma (1973) trapped many in pine flatwoods, and lesser numbers in a sand-pine dune or in citrus groves.

Courtship behavior was described (under the name *banksi*) by Kaston (1936). The present authors observed adults running on a salt marsh in Nova Scotia on a warm day at the end of May, 1980. Males and females were seen on or under the mat of dry marsh grasses, particularly at the water's edge where the mud was wet from the previous tide. If overtaken by a wave they either ran on its surface or climbed emergent plant stems.

Comments on Synonymy. This spider has been variously known under five specific names, one of which was proposed on the assumption that the name *littoralis* was preoccupied in *Pardosa.* Chamberlin (1904) apparently did not realize that the name *Lycosa littoralis* Walckenaer, 1805 was a *nomen nudum* and, therefore, not available. He was apparently also unaware of the older available names *Pardosa longispinata* Tullgren, 1901 and *Pardosa floridana* Banks, 1904.

Pardosa saltonia sp.n.
Figures 23, 26, 62–64; Map 6

Type Material. Holotype male from Fish Springs, west side of Salton Sea, Imperial County, California, 116° 02'W, 33° 25'N, 12 March 1941 (Wilton Ivie), deposited

in AMNH. Two paratype males and 13 paratype females from the type locality (same data as holotype), in AMNH. One paratype female from northeast shore of Salton Sea, 8 October 1963 (Jean and Wilton Ivie), in AMNH. One paratype female from east shore of Salton Sea, 23 September 1957 (Vince Roth), in AMNH. Two paratype males and 1 paratype female from Salton Sea, 26 September 1964 (Vince Roth), in AMNH. One paratype female from Salton, California, in MCZ. Seven paratype males and 5 paratype females from La Choya, Sonora, 12 June 1952 (W. J. Gertsch), in AMNH.

Male. Total length 6.39 ±0.35 mm; carapace 3.15 ±0.13 mm long and 2.46 ±0.12 mm wide (12 specimens). Carapace with yellow orange median and submarginal areas, and with pair of dark longitudinal bands flanking median area; margins dark. Sternum orange yellow, suffused with black, or entirely black. Chelicerae orange brown; retromargin with 2 teeth (rarely with small third tooth on one or both chelicerae). Legs dark yellow orange. Abdomen yellow orange mesally, dark laterally; venter pale. Terminal apophysis arched retrolaterally; median apophysis small, occupying only about one-third length of genital bulb (Fig. 23); conductor with single curve on basal margin, with dark, shiny knob near tip (Fig. 26).

Female. Total length 7.54 ±1.04 mm; carapace 3.39 ±0.34 mm long and 2.71 ±0.27 mm wide (20 specimens). General color and structure as in male but paler. Epigynum rather short, with ratio of length to greatest width of median septum less than 2:1; septum abruptly narrowed anteriorly from widest point (Fig. 62); copulatory tubes curved to nearly straight, with swelling on ventral or lateral margin (Figs. 63, 64).

Diagnosis. Specimens of *P. saltonia* differ from those of the other species in the *milvina* group by the retrolaterally arched terminal apophysis, by the small median apophysis (occupying about one-third the genital bulb length), by the short epigynum and abruptly narrowed median septum (ratio of epigynal length to greatest median septum width less than 2:1), and in part by the presence of 2 teeth on the cheliceral retromargin.

Range. Salton Sea area of California; Sonora.

Natural History. Males of *saltonia* have been collected in March, June, and December, and females in March, June, September, October, and December. Egg sacs were found in March and September.

Derivation of Specific Name. The name is derived from that of the Salton Sea.

Pardosa pauxilla Montgomery
Figures 24, 27, 65–67; Map 4

Pardosa pauxilla Montgomery, 1904:268, Figs. 22, 23 (pl. 19). Lectotype male from Austin, Texas, deposited in AMNH and here designated. One paralectotype female from the type locality, in AMNH. One paralectotype male from the type locality, in MCZ. One female, part of the syntype series, deposited in MCZ, represents *Pardosa delicatula* Gertsch and Wallace. Other syntypes not found. Chamberlin 1908:180, Fig. 9 (pl. 13). Petrunkevitch 1911:574. Gertsch and Wallace 1935:4, Figs. 11, 15. Muma 1945:22; 1973:179; 1975:86. Bonnet 1958:3406. Berry 1970:102. Howell and Pienkowski 1971:164.

Pardosa uncatula: Gertsch 1934:20 (part). Roewer 1954:190 (part).

Pardosa georgiae Chamberlin and Ivie, 1944:147, Figs. 185, 186 (pl. 13). Holotype female from Savannah Beach, Georgia, 80°51′W, 32°0′N, 4 May 1943 (Wilton Ivie), deposited in AMNH, examined. One paratype male from the type locality, same data, in AMNH, examined. One paratype male and 3 paratype females from the type locality, same data, not found. Wallace 1950:78, Figs. 1, 2 (pl. 1). Roewer 1954:191. Vogel 1967:104. **NEW SYNONYM.**

Male. Total length 4.24 ±0.26 mm; carapace 2.26 ±0.17 mm long and 1.67 ±0.11 mm wide (20 specimens). Carapace usually with yellow orange median and submarginal areas, and with paired dark, longitudinal bands flanking median area; margins usually pale. Sternum dark yellow or yellow brown, sometimes with small black spots along margins. Chelicerae pale yellow brown to black; retromargin with 3 teeth. Legs orange yellow; femur I (and sometimes II) often dark on basal three-fourths. Abdomen dull black, sometimes dull yellow mesally; venter pale yellow, sometimes with faint darker median band. Terminal apophysis with mesal swelling toothlike; median apophysis thick throughout most of its length, with basal process swollen (Fig. 24); conductor with single curve on basal margin, with dark, shiny knob near tip (Fig. 27). Female. Total length 5.05 ±0.55 mm; carapace 2.39 ±0.25 mm long and 1.79 ±0.13 mm wide (20 specimens). General color and structure as in male but paler. Median septum distinctly tapered anteriorly, with expanded posterior part concave at lateral margins (Fig. 65); copulatory tubes rather stout, with swellings on ventral surfaces (Figs. 66, 67).

Diagnosis. Specimens of *P. pauxilla* differ from those of the other species in the *milvina* group by the toothlike swelling mesal to the

terminal apophysis, by the large, swollen basal process on the median apophysis, and by the long, distinctly tapered median septum of which the posterior expanded part has concave lateral margins.

Range. Kansas to New Jersey, south to New Mexico, southern Texas, and Florida.

Natural History. Males and females have been collected in every month except December. Egg sacs were collected from March to May and from July to November. The commonest habitat is grassy pastures, but many specimens have been taken at stream or pond margins or in crops such as alfalfa, soybeans, sweet potatoes, and peanuts. Muma (1973) trapped specimens in citrus groves and pine flat-woods in Florida.

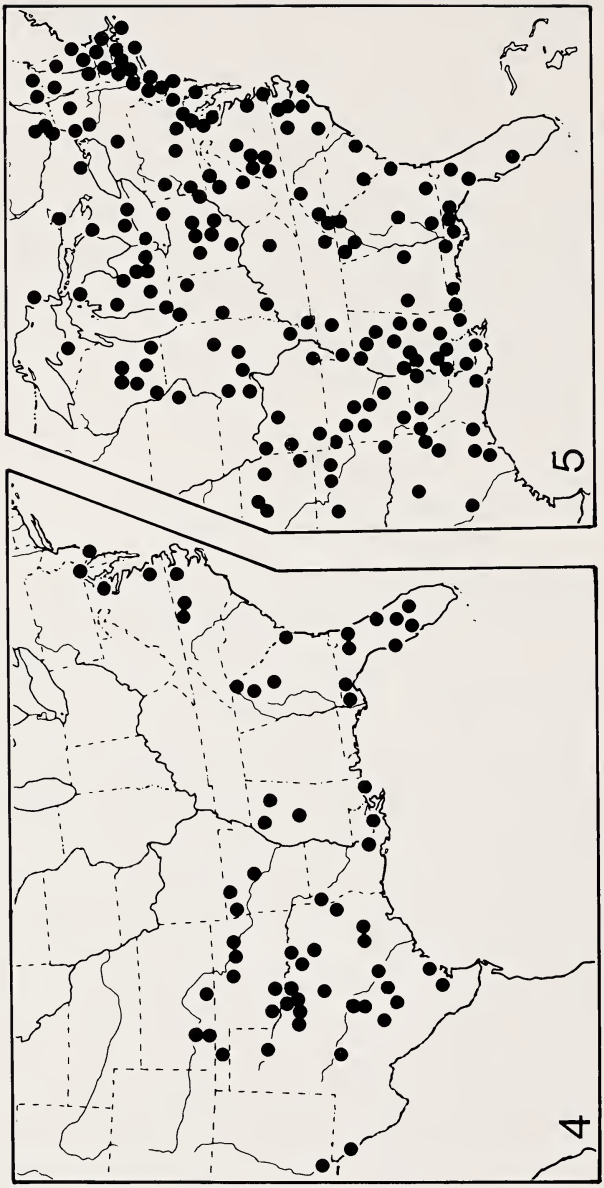
Pardosa portoricensis Banks
Figures 28, 29, 68, 69

Pardosa porto-ricensis Banks, 1902:224, Figs. 2, 3 (pl. 15). Holotype female from San Juan, Puerto Rico, 1–10 January 1899 (August Busck), deposited in USNM, examined.

Pardosa portoricensis: Petrunkevitch 1911:574; 1929:87, Figs. 74, 75. Roewer 1954:188. Bonnet 1958:3407.

Male. Total length 3.56 mm; carapace 2.00 mm long and 1.56 mm wide (1 specimen). Carapace with orange yellow median and submarginal areas, and with pair of distinct dark, longitudinal bands flanking median area; margins somewhat dark. Sternum pale yellow. Chelicerae pale orange, lightly marked with gray; retromargin with 3 teeth. Legs pale yellow. Abdomen pale mesally, with pair of dark longitudinal bands laterally. Terminal apophysis small, pointed; median apophysis with distal process expanded (ventral view, Fig. 28); conductor curved on basal margin, with dark shiny knob near tip (Fig. 29).

Female. Total length 4.51 ±0.70 mm; carapace 2.24 ±0.26 mm long and 1.79 ±0.23 mm wide (16 specimens). General color and structure as in male. Epigynum rather long (ratio of epigynum length to greatest septal width more than 2:1) (Fig. 68); median septum tapered and indistinct anteriorly; copulatory tubes slender, and spermathecae narrowly separated (Fig. 69).



Map 4. Collection localities for *Pardosa pauxilla*.

Map 5. Collection localities for *Pardosa milvina*.

Diagnosis. Specimens of *P. portoricensis* differ from those of the other West Indian species in the *milvina* group by the expanded distal process of the median apophysis, by the longitudinally banded abdominal dorsum, by the long epigynum (ratio of epigynal length to greatest septal width more than 2:1), by the anteriorly tapered median septum, and by the slender copulatory tubes and narrowly separated spermathecae.

Localities. PUERTO RICO: San Juan; Mayaguez; Martin Pena; Puerto Nuevo Point, near Vega Baja; Embarcadero Point, near Luquillo. VIRGIN ISLANDS: St. Croix: Chistiansted. ANTIGUA: Lignum Vitae Bay: Reed Point, Jolly Beach.

Range. Puerto Rico, Virgin Islands, and western Antigua.

Natural History. The only available male was collected with females in October. Other females were collected in January to March and in June. Egg sacs were found in June, and one of the October females carried young. Petrunkevitch (1929) collected specimens on the "sandy plains" of the northern coast of Puerto Rico.

Pardosa milvina (Hentz)
Figures 30–32, 70, 71; Map 5

Lycosa milvina Hentz, 1844:392, Fig. 8 (pl. 18). Holotype female from Alabama, September, destroyed. Hentz 1875:33, Fig. 8 (pl. 4).

Lycosa flavipes Keyserling, 1877:616, Fig. 4 (pl. 7). Syntype female from Peoria, Illinois, deposited in BM(NH), examined. Syntype female from Baltimore, Maryland, not found.

Pardosa nigropalpis Emerton, 1885:497, Figs. 1, 1*a*–1*d* (pl. 49). Five syntype males and 1 syntype female from New Haven, Connecticut, 25 May 1883 (J. H. Emerton), deposited in MCZ, examined. Syntypes from Massachusetts, not found. Emerton 1902:83, Figs. 202–204. Stone 1890:430. Banks 1892:70; 1893:125. Montgomery 1902:569, Figs. 32–34 (pl. 30); 1904:275. Scheffer 1905*a*:119; 1905*b*:191. Bryant 1908:89. Barrows 1918:315. Roewer 1954:193.

Pardosa milvina: Banks 1899:189; 1904*a*:135; 1904*b*:115, Fig. 6 (pl. 5). Scheffer 1906:126. Chamberlin 1908:177, Figs. 3, 4 (pl. 13). Petrunkevitch 1911:572. Gertsch and Wallace 1935:5, Figs. 19, 20. Comstock 1940:662, Figs. 731*i*, 732*e*. Muma 1945:22. Kaston 1948:334, Figs. 1100–1103 (pl. 56), 1138 (pl. 59); 1978:190, Fig. 486. Levi and Field 1954:456. Roewer 1954:192. Bonnet 1958:3388. Fitch 1963:113. Berry 1970:102. Howell and Pienkowski 1971:164. Wolff 1981:64.

Pardosa scita Montgomery, 1902:573, Figs. 37, 38 (pl. 30). One syntype male and 1 syntype female from Philadelphia, Pennsylvania, deposited in AMNH, examined. Montgomery 1904:272.
Pardosa canadensis: Banks 1910:58 (part); 1916:81 (part). Bonnet 1958:3362 (part).

Male. Total length 4.64 ±0.36 mm; carapace 2.40 ±0.20 mm long and 1.91 ±0.15 mm wide (20 specimens). Carapace with yellow orange median and submarginal areas, and with paired black longitudinal bands flanking median area; margins often pale. Sternum yellow to nearly black. Chelicerae pale to dark yellow brown; retromargin with 3 teeth. Legs orange yellow; femur I sometimes black on basal half. Abdomen yellow brown, much mottled with black; venter pale yellow, often lightly spotted or lined with black. Terminal apophysis broad, blunt; median apophysis slender at middle, with distal process slender (Figs. 30, 31); conductor curved on basal margin, with dark, shiny knob near tip (Fig. 32).
Female. Total length 5.77 ±0.65 mm; carapace 2.73 ±0.25 mm long and 2.16 ±0.19 mm wide (20 specimens). General color and structure as in male but legs more distinctly ringed and abdominal dorsum sometimes with paried, indistinct longitudinal bands; femur I lacking black area in basal half. Median septum extending anteriad less than one-half length of epigynum; hood continuing posteriad at sides where it defines a depressed, non-tapered area (Fig. 70); copulatory tubes rather slender, with lateral swellings (Fig. 71).

Diagnosis. Specimens of *P. milvina* are distinguished from those of the other species in the *milvina* group by the combination of terminal apophysis small, broad, blunt, arched mesally, and lacking a toothlike mesal swelling, median apophysis slender at middle and with a slender distal process, short median septum, hood extending posteriad at sides where it defines a depressed, non-tapered area, and occurrence only north of the Tropic of Cancer (approximately 23° 30′N).

Range. Northern Peninsula of Michigan and southern Ontario to southern Québec and Maine, south to Texas and Florida.

Natural History. Males of *P. milvina* have been collected from February to August, and females from February to November. Egg sacs were recorded from April to September. The species appears to

reach high densities in moist habitats such as swamps, meadows, mud flats, and edges of creeks and ponds, but is also found in deciduous and cedar woods, lawns, gardens, pastures, and various crops (rice, corn, cotton, sweet potato, soybean, alfalfa). Montgomery (1903) and Kaston (1936) described courtship and copulatory behavior.

Pardosa guadalajarana sp.n.
Figures 33–35, 72, 73; Map 6

Type Material. Holotype male from 4 miles southwest of Guadalajara, Jalisco, Mexico, 20 June 1941 (L. I. Davis), deposited in AMNH. Three paratype males and three paratype females from the type locality (same data as holotype), deposited in AMNH. One paratype male and fourteen paratype females from localities other than the type locality, in Mexico and Honduras, deposited in AMNH.

Male. Total length 3.03–3.18 mm; carapace 1.62–1.70 mm long and 1.21–1.30 mm wide (5 specimens). Carapace black, with dark orange brown median area. Sternum dark orange brown suffused with black. Chelicerae black, with dull yellow area anteromesally; retromargin with 2 teeth. Legs orange brown, with femora often darkened or with 2 or 3 dark, indistinct rings. Abdomen dark red brown, spotted with black, and with median band of reflective white setae; venter dull yellow, sometimes with small black spots. Terminal apophysis pointed; median apophysis abruptly angled on mesal margin (Figs. 33, 35); conductor with single curve along basal margin, with dark knob near tip (Fig. 34).

Female. Total length 3.96 ±0.36 mm; carapace 1.86 ±0.08 mm long and 1.42 ±0.11 mm wide (16 specimens). General color and structure as in male but carapace usually much paler, the carapace with pale median band distinct and margins pale, and abdomen lacking band of reflective white setae. Median septum extending approximately three-fourths length of epigynum; posterior part more or less triangular, concave at lateral margins, and rather narrow (ratio of epigynal length to greatest septum width more than 2:1) (Fig. 72); copulatory tubes slender, with lateral swellings (Fig. 73).

Diagnosis. Specimens of *P. guadalajarana* most resemble those of *P. longivulva* and *P. marialuisae* but differ in the abruptly angled median apophysis, in the possession of two retromarginal teeth on the chelicera, and in the small size.

Range. Jalisco to the Honduras/El Salvador border.

Natural History. Males have been collected in June and July, and females June to August. No habitat data are recorded.

Derivation of Specific Name. The name is derived from that of the city of Guadalajara.

Pardosa longivulva F. Pickard-Cambridge
Figures 36–38, 74, 75; Map 6

Pardosa longivulva F. Pickard-Cambridge, 1902:318, Figs. 21, 21*a*, 22 (pl. 30). Holotype female from Teapa, Tabasco, Mexico (H. H. Smith), deposited in BM(NH), examined. Two paratype males from the type locality (same vial as holotype), in the same institution, examined. One female from the type locality (same vial as holotype and paratypes) is *Pardosa hamifera* F. Pickard-Cambridge. Paratype from Amula, Guerrero, Mexico, not found. Petrunkevitch 1911:572.

Pardosa longivulvula Roewer, 1951:440. New name for *Pardosa longivulva*, proposed on the mistaken assumption that the latter was preoccupied.

Male. Total length 4.31–4.50 mm; carapace 2.08–2.49 mm long and 1.72–2.03 mm wide (6 specimens). Carapace with orange median and submarginal areas, and with paired dark, longitudinal bands flanking median area; margins black. Sternum dark orange, often with scattered black spots or with median black band. Chelicerae dark orange brown to black; retromargin with 3 teeth. Legs yellow orange; femur I sometimes with black area at base; tibia and basitarsus I with fringe of long, erect, dark setae on prolateral and retrolateral surfaces. Abdomen black to yellow brown, darker laterally; venter off-white to yellow brown, sometimes with many dark dots or with one to three dark longitudinal bands. Terminal apophysis long, rather slender; median apophysis slender at middle, with slender distal process (Figs. 36, 37); conductor with single curve along basal margin, with dark knob near tip (Fig. 38).

Female. Total length 4.98–5.47 mm; carapace 2.58–2.80 mm long and 1.96–2.42 mm wide (4 specimens). General color and structure

as in male but carapace with pale areas more extensive and leg I lacking dark area at base and lacking setal fringe. Epigynum rather long (ratio of epigynal length to greatest septal width more than 2:1); median septum with expanded posterior part approximately triangular in outline and concave at lateral margins (Fig. 74); copulatory tubes with small swellings at base (Fig. 75).

Diagnosis. Specimens of *P. longivulva* can be distinguished from those of the other species in the *milvina* group by the combination of black carapace margins, presence of a setal fringe on tibia and basitarsus I of males, rather long and slender terminal apophysis, long epigynum (ratio of epigynal length to greatest septal width more than 2:1), small swellings at base of copulatory tubes, and occurrence restricted south of the Tropic of Cancer.

Range. Tabasco, Mexico to Guatemala.

Natural History. Adults have been collected in February, March, and June. One of the females collected in February had an egg sac. Habitat is not recorded.

Pardosa marialuisae sp.n.
Figures 39, 40, 42, 76, 77; Map 6

Type Material. Holotype male from Pico de Oro, 93°30′W, 17°58′N, Tabasco, Mexico, 12 August 1966 (Jean and Wilton Ivie), deposited in AMNH. Paratype female from the type locality (same data as holotype), in AMNH. Twenty-four paratype males and 33 paratype females from Mexico and Honduras, deposited in AMNH. Five paratype males and 17 paratype females from Guatemala, deposited in MCZ.

Male. Total length 3.85 ±0.20 mm; carapace 2.04 ±0.10 mm long and 1.57 ±0.12 mm wide (20 specimens). Carapace usually black, with margins alone pale, but rarely with pale submarginal areas and dark margins. Sternum orange yellow, sometimes with small black spots at posterior and lateral margins. Chelicerae usually black, more rarely yellow orange; retromargin with 3 teeth. Legs yellow orange; femur I sometimes with black area at base. Abdomen yellow orange to black; if pale, then mottled or spotted, and darkest along lateral margins; venter pale yellow, sometimes spotted with black.

Map 6. Collection localities for *Pardosa saltonia* (triangles), *P. quadalajarana* (half-circles), *P. longivulva* (stars), *P. marialuisae* (circles).

Terminal apophysis slender, pointed, rather short; median apophysis slender at middle, with slender distal process (Figs. 39, 42); conductor curved on basal margin, with dark, shiny knob near tip (Fig. 40).

Female. Total length 4.80 ±0.64 mm; carapace 2.30 ±0.18 mm long and 1.88 ±0.19 mm wide (20 specimens). General color and structure as in male but with pale mesal area on carapace, and with front and chelicerae pale. Epigynum long (ratio of total length to greatest median septum width more than 2:1); median septum with expanded posterior part approximately triangular, concave at sides (Fig. 76); copulatory tubes with large swellings at lateral margins (Fig. 77).

Diagnosis. Specimens of *P. marialuisae* can be distinguished from the other members of the *milvina* group by the combination of usually pale carapace margins, lack of a setal fringe on leg I, the possession of a rather short, pointed terminal apophysis, long epigynum (ratio of epigynal length to greatest septal width more than 2:1), large swellings at the sides of the copulatory tubes, and occurrence restricted south of the Tropic of Cancer.

Range. Hidalgo, Mexico to Honduras.

Natural History. Males have been collected from February to August and in October, females from January to August and in October. Egg sacs were collected in May and August. The only habitat recorded on the labels is "along river" at 30 miles southeast of Palenque Aqua Azul, Chiapas, Mexico.

Derivation of Specific Name. The name is derived from that of our friend and colleague Maria-Luisa Jiménez of Universidad Nacional Autónoma de México.

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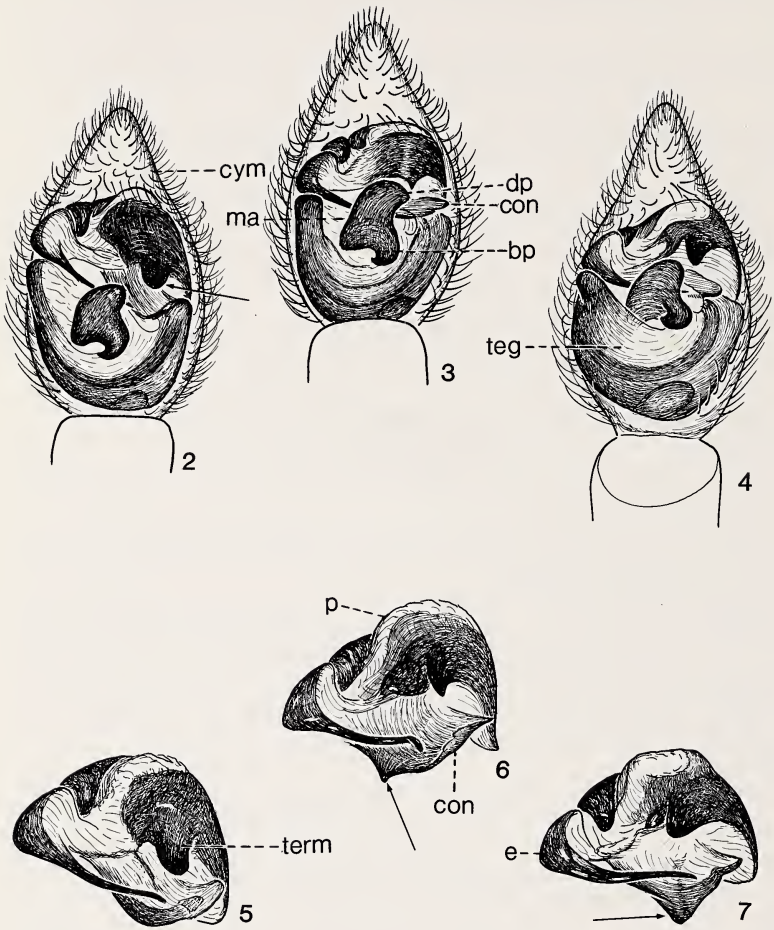
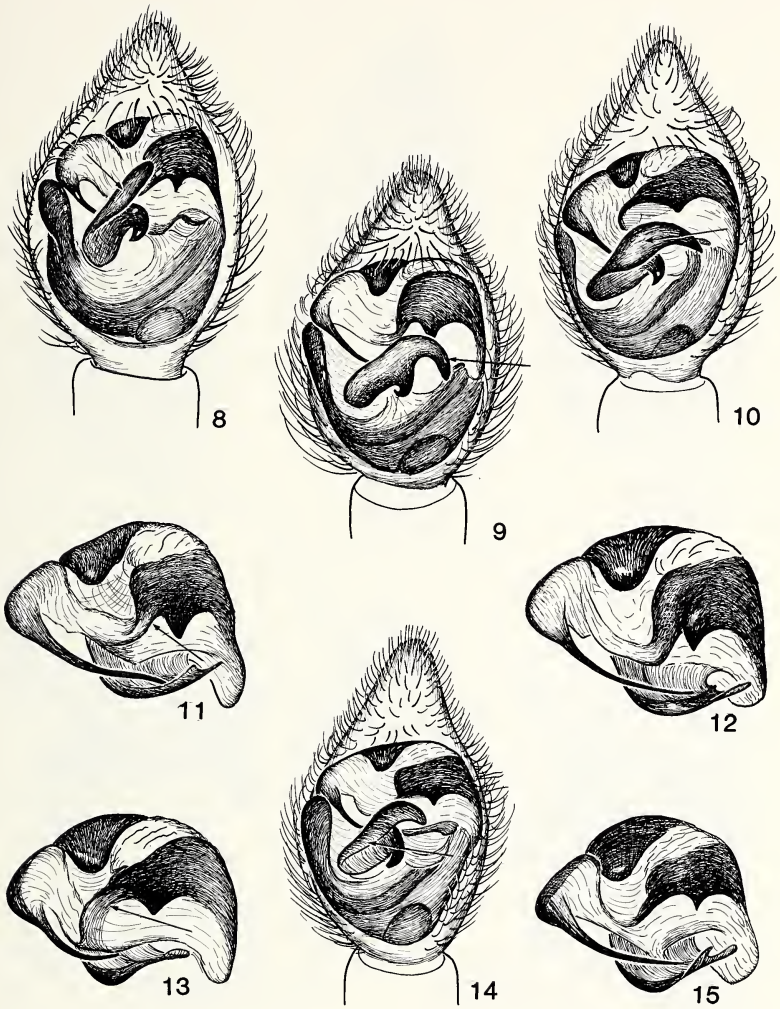
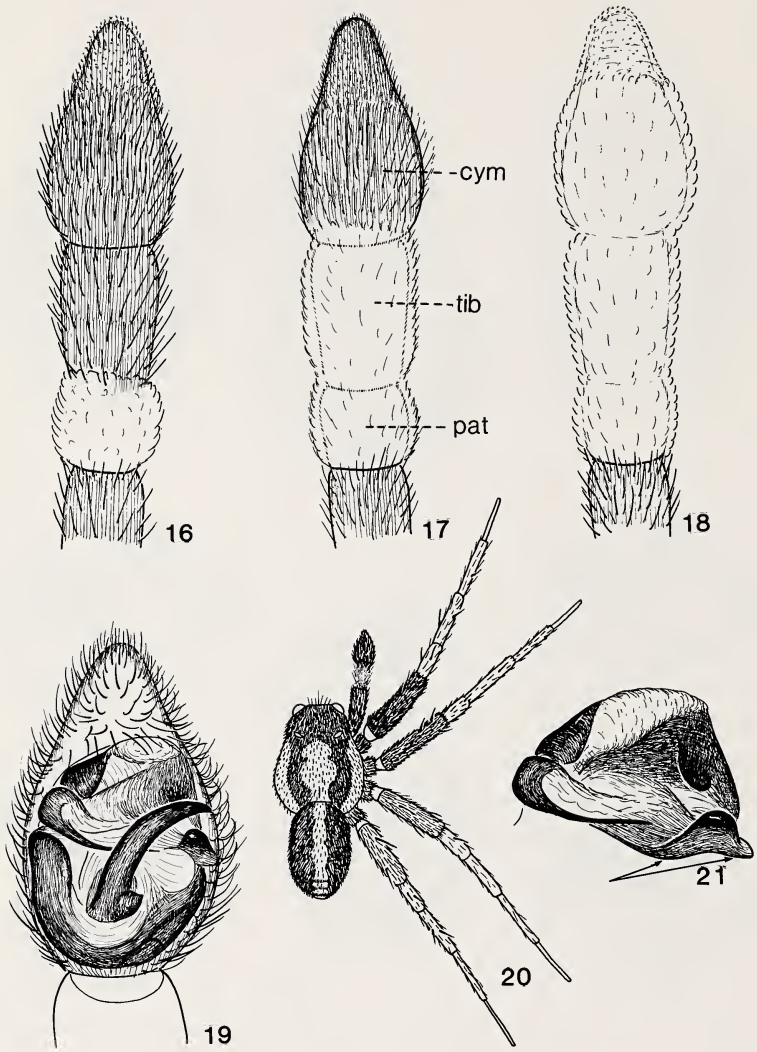


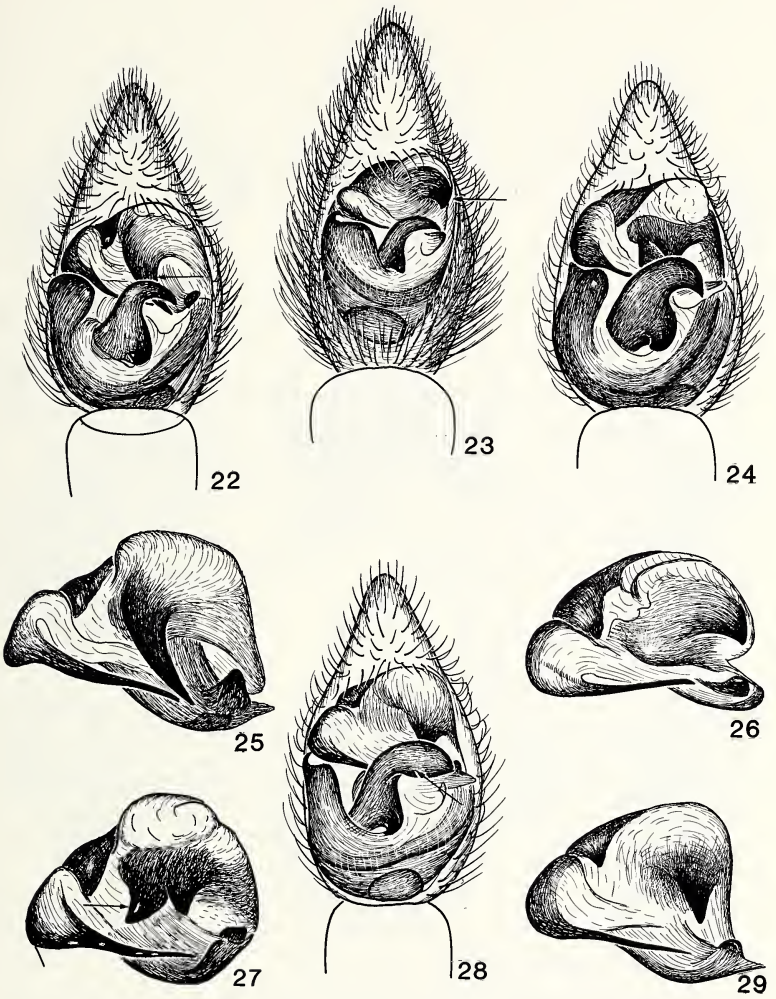
Figs. 2–7. External male genitalia of *Pardosa* spp. 2–4, palpus, ventral view. 5–7, apical division, ventral view. 2,5, *P. bellona* Banks. 3,6, *P. delicatula* Gertsch and Wallace. 4,7, *P. hamifera* F. Pickard-Cambridge. *bp,* basal process of median apophysis. *con,* conductor. *cym,* cymbium. *dp*, distal process of median apophysis. *e,* embolus. *ma,* median apophysis. *p,* palea. *teg,* tegulum. *term,* terminal apophysis.



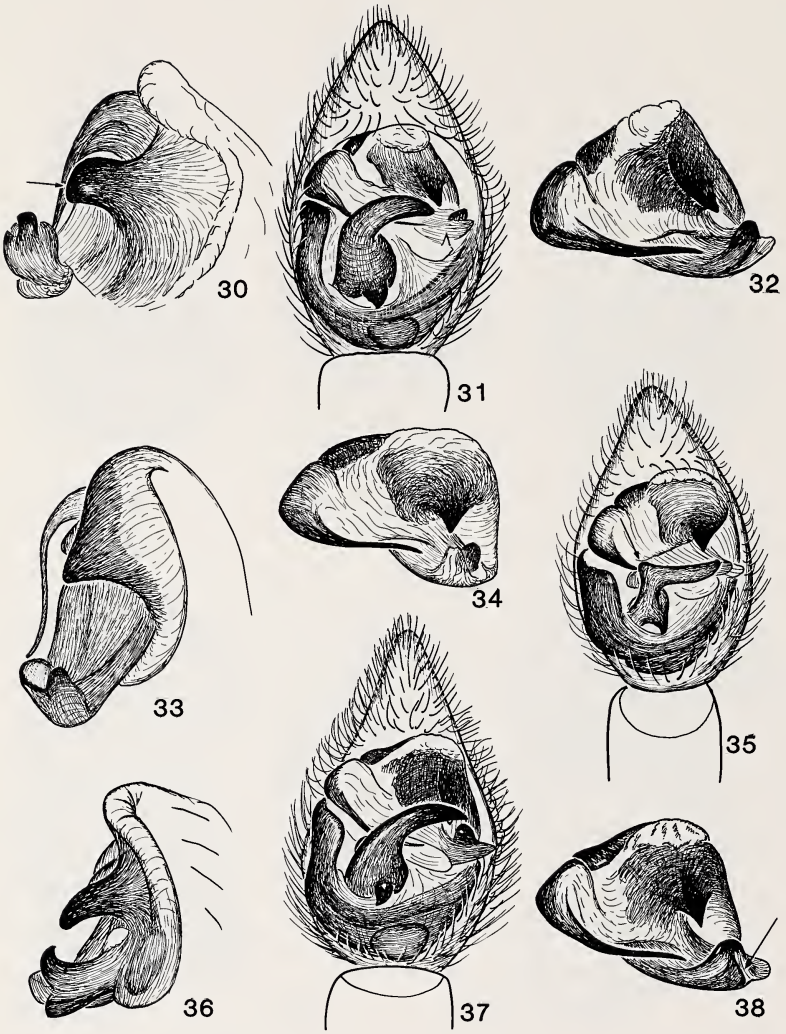
Figs. 8–15. External male genitalia of *Pardosa* spp. 8–10,14, palpus, ventral view. 11–13,15, apical division, ventral view. 8,11, *P. sagei* Gertsch and Wallace. 9,12, *P. fastosa* (Keyserling). 10,13, *P. desolatula* Gertsch and Davis. 14,15, *P. mayana* sp.n.



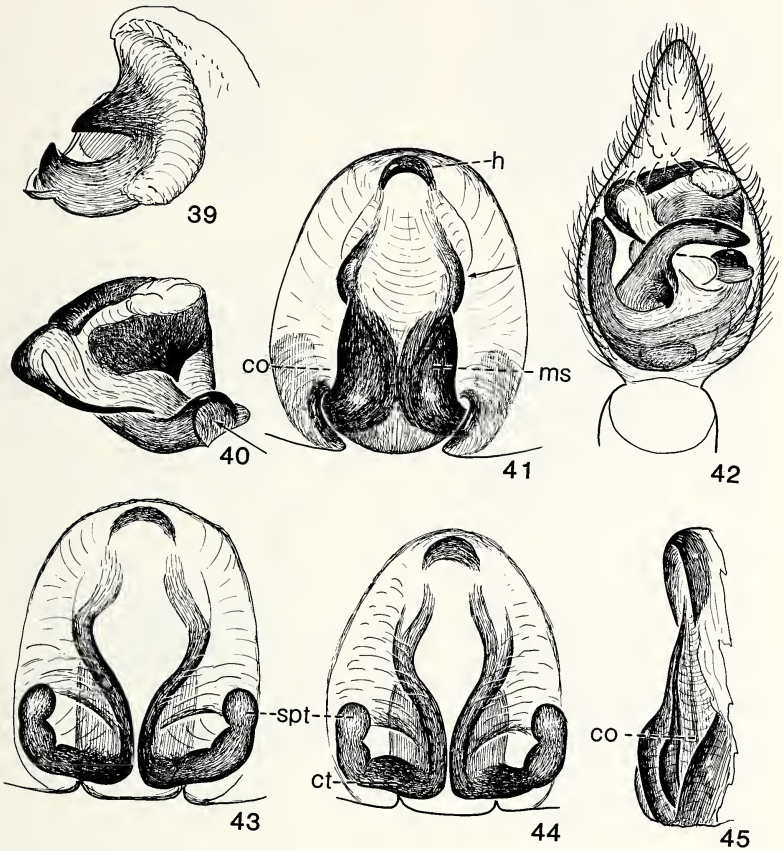
Figs. 16–21. Male structures of *Pardosa* spp. 16–18, palpus, dorsal view. 19, palpus, ventral view. 20, body, dorsal view. 21, apical division, ventral view. 16,19–21, *P. saxatilis* (Hentz). 17, *P. atlantica* Emerton. 18, *P. parvula* Banks.



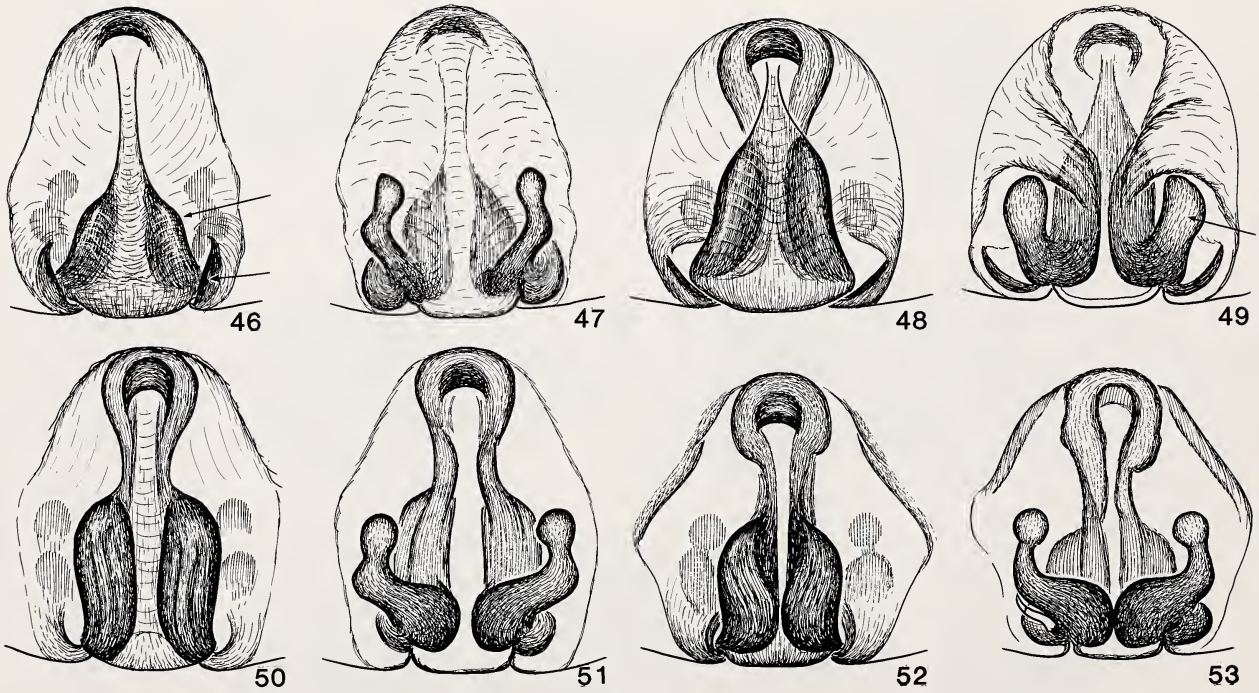
Figs. 22–29. External male genitalia of *Pardosa* spp. 22–24, 28, palpus, ventral view. 25–27,29, apical division, ventral view. 22,25, *P. littoralis* Banks. 23,26, *P. saltonia sp. n.* 24,27, *P. pauxilla* Montgomery. 28,29, *P. portoricensis* Banks.



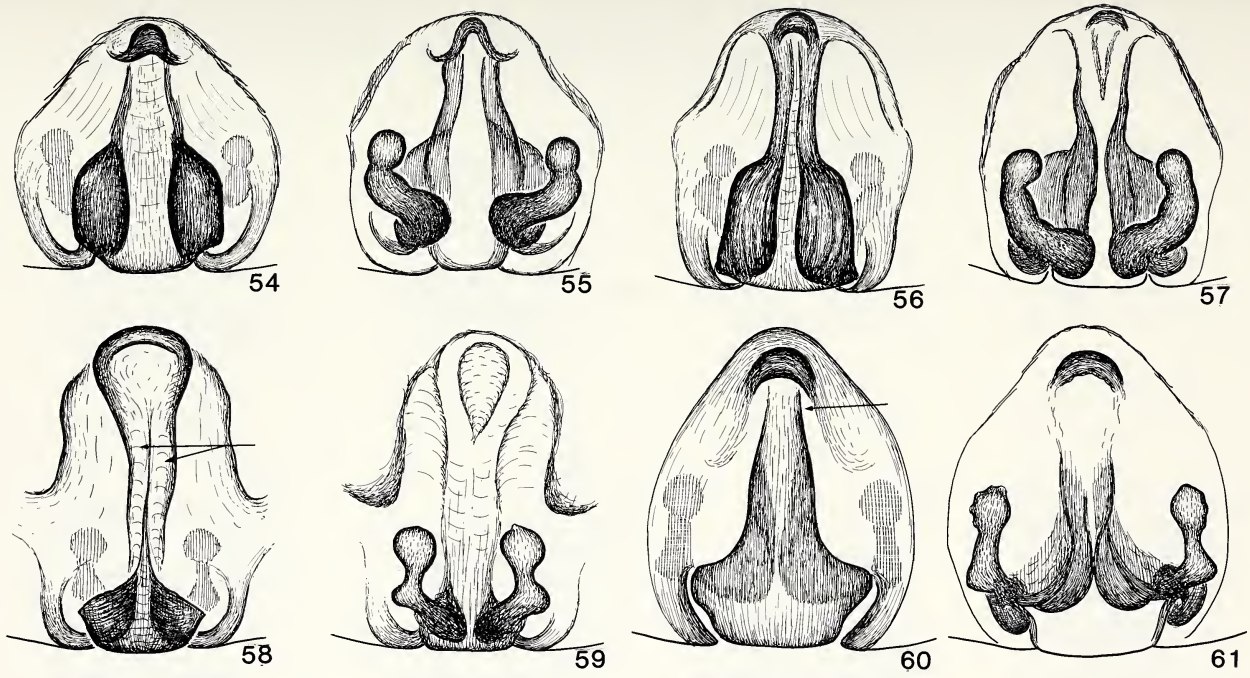
Figs. 30–38. External male genitalia of *Pardosa* spp. 30,33,36, apical division, retrolateral view. 31,35,37, palpus, ventral view. 32,34,38, apical division, ventral view. 30–32, *P. milvina* (Hentz). 33–35, *P. guadalajarana* sp. n. 36–38, *P. longivulva* F. Pickard-Cambridge.



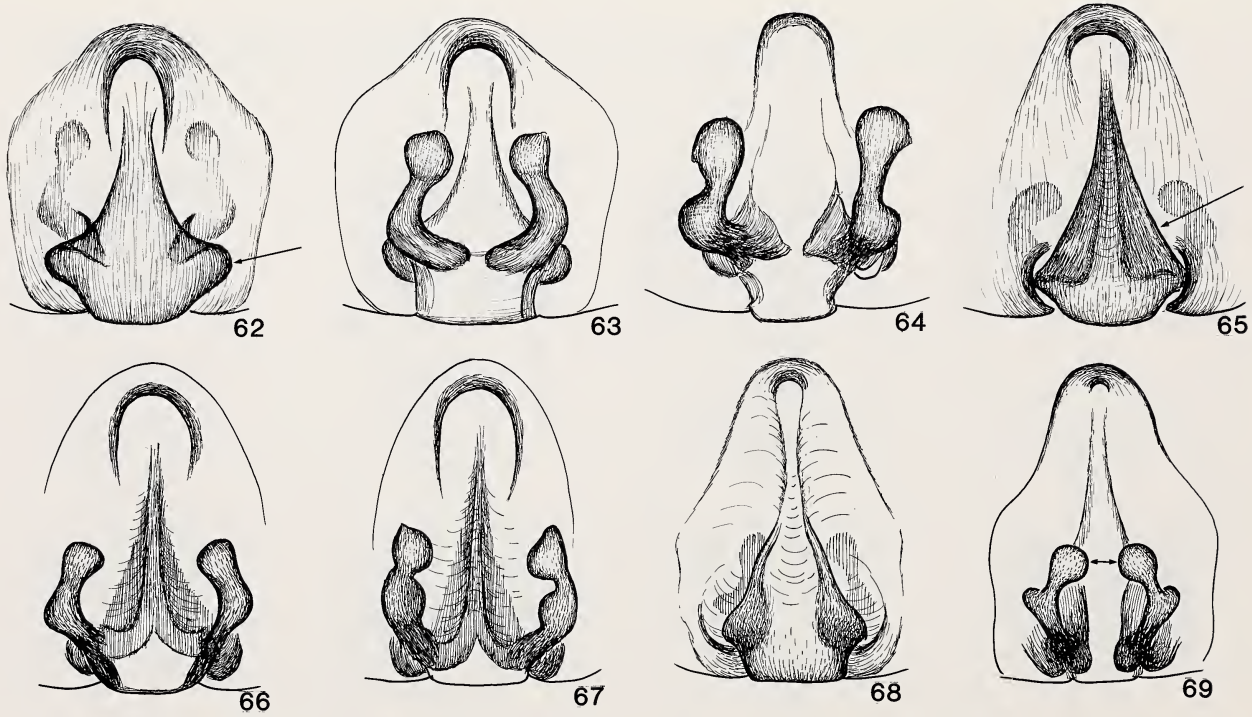
Figs. 39–45. External male genitalia of *Pardosa* spp. 39, apical division, retrolateral view. 40, apical division, ventral view. 42, male palpus, ventral view. 41,43–45, epigynums. 41, ventral view. 43,44, dorsal view. 45, lateral view. 39,40,42, *P. marialuisae* sp. n. 41, 43, 44, *P. bellona* Banks. 45, *P. delicatula* Gertsch and Wallace. *co,* copulatory opening. *ct,* copulatory tube. *h,* hood. *ms.* median septum. *spt,* spermathecae.



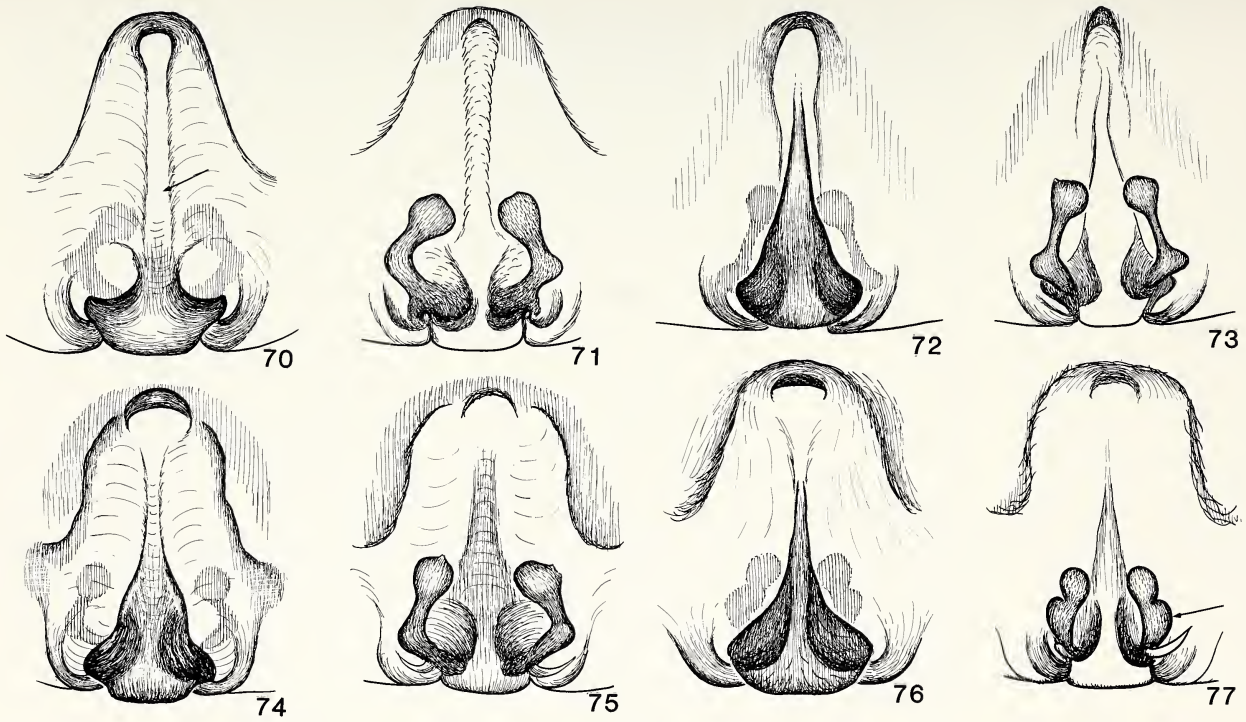
Figs. 46–53. Epigynums of *Pardosa* spp. 46,48,50,52, ventral view. 47,49,51,53, dorsal view. 46,47, *P. delicatula* Gertsch and Wallace. 48,49, *P. hamifera* F. Pickard-Cambridge. 50, 51, *P. sagei* Gertsch and Wallace. 52,53, *P. fastosa* (Keyserling).



Figs. 54–61. Epigynums of *Pardosa* spp. 54,56,58,60, ventral view. 55,57,59,61, dorsal view. 54,55, *P. desolatula* Gertsch and Davis. 56,57, *P. mayana* sp. n. 58, 59, *P. saxatilis* (Hentz). 60,61, *P. littoralis* Banks.



Figs. 62–69. Epigynums of *Pardosa* spp. 62,65,68, ventral view. 63,64,66,67,69, dorsal view. 62–64, *P. saltonia* sp. n. 65–67, *P. pauxilla* Montgomery. 68, 69, *P. portoricensis* Banks.



Figs. 70–77. Epigynums of *Pardosa* spp. 70,72,74,76, ventral view. 71,73,75,77, dorsal view. 70,71, *P. milvina* (Hentz). 72,73, *P. guadalajarana* sp. n. 74,75, *P. longivulva* F. Pickard-Cambridge. 76,77, *P. marialuisae* sp. n.

THE IDENTITY OF *CHAETOCLUSIA AFFINIS* JOHNSON AND ITS PLACEMENT IN *SOBAROCEPHALA* CZERNY (DIPTERA: CLUSIIDAE)*

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Johnson (1913) described *Chaetoclusia affinis* on the basis of one male and one female from New Jersey. His brief and inadequate description has not allowed subsequent authors to recognize the species and omits discussion of characters later used to define clusiid genera. Melander and Argo (1924) simply repeated Johnson's description and mentioned that they had not seen his material.

I have recently examined the holotype male and allotype female of *C. affinis,* which are housed in the Museum of Comparative Zoology at Harvard University (MCZ #7873). It was readily apparent that Johnson had placed the species in the wrong genus, and that *C. affinis* actually belongs in the genus *Sobarocephala* Czerny, not *Chaetoclusia* Coquillett. Both of Johnson's specimens lack the longer, bristle-like hairs on wing vein R_1, which are characteristic of *Chaetoclusia.* Johnson probably placed the species in *Chaetoclusia* because of its densely pubescent antennal arista, a character state found in *Chaetoclusia bakeri* Coquillett, the type species of the genus. This feature, however, is not unique to *Chaetoclusia,* and in fact partially defines the "plumata" species group of *Sobarocephala,* as recognized by Soós (1963).

When *S. affinis* is run through the most recent key to Nearctic *Sobarocephala* (Sabrosky and Steyskal, 1974), it runs without difficulty to *S. testacea* Soós. The holotype male of *S. testacea,* housed in the U. S. National Museum of Natural History, was recently examined and found to be conspecific with *S. affinis.* Johnson's allotype is probably also conspecific, but there is difficulty in separating females of this species from those of *S. muesebecki* Sabrosky and Steyskal. The latter species is known with

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certainty from Florida, and from a questionable specimen from Maryland (see Sabrosky and Steyskal, 1974: 378).

As a result of this study, the following nomenclatural changes result:

Sobarocephala affinis (Johnson), 1913: 101. NEW COMBINATION.
Sobarocephala testacea Soós, 1964: 449. NEW SYNONYMY.

The holotype of *Chaetoclusia affinis* Johnson is in poor condition. It is missing the head and the legs beyond the trochanters, except that the right front femur and tibia are present. I have removed and cleared most of the abdomen, including the male terminalia, and placed them in glycerin in a microvial on the specimen pin, so that they will be better preserved and more useful for future workers. Due to the absence of the head, the male genitalia are the only features of the type that will allow conclusive identification of the specimen.

Because *C. affinis* Johnson really belongs in *Sobarocephala,* this deletes the only species ascribed to *Chaetoclusia* from the Nearctic fauna. The genus is now known only from the Neotropical Region extending from Nicaragua south to Peru, and also Haiti and St. Vincent (Soós, 1968). It seems unlikely that the genus will be found in the Nearctic Region, although its Caribbean distribution makes it just possible that it might someday be found in southern Florida.

I wish to thank Wayne Mathis, Department of Entomology, Smithsonian Institution, and D. R. Miller, Systematic Entomology Lab, USDA, for reviewing the manuscript.

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THE INFLUENCE OF MICROHABITAT AND PREY AVAILABILITY ON BURROW ESTABLISHMENT OF YOUNG *GEOLYCOSA TURRICOLA* (TREAT) AND *G. MICANOPY* WALLACE (ARANEAE: LYCOSIDAE): A LABORATORY STUDY*

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Introduction

The survival of an animal largely depends on its ability to locate and use a suitable habitat. The suitability of a habitat will depend on such things as prey availability, microhabitat characteristics and the interaction of these,but our understanding of the interaction of these factors and how they effect the animal's choice of habitat is poor (Krebs, 1978).

For spiders, there have been many studies which show the importance of habitat characteristics and prey abundance in the selection of foraging and web sites (e.g., Savory, 1930; Enders, 1977; Riechert, 1976; Riechert and Tracy, 1975). However, most studies deal with adult spiders (some exceptions being the work of Waldorf, 1976; Enders, 1977 and Hallander, 1970) and our understanding of which factors may influence habitat selection in newly dispersing young spiders is limited. These factors are particularly important for burrowing wolf spiders (*Geolycosa*) since the selected burrow site is generally used throughout the life of the spider (Wallace, 1942). In this paper I test selected hypotheses about the interactions among burrow establishment, prey availability, and several microhabitat characteristics in two species of burrowing wolf spiders. This paper is not concerned with the relationship between the burrow site characteristics and survival of the spiderling, which is best studied in the field (see Reichert, 1976 and Reichert and Tracy, 1975 for

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examples of elegant field studies concerning habitat selection and survival).

Geolycosa spp. are obligate burrowers which establish a burrow shortly after leaving the mother (Wallace, 1942; McCrone, 1964; pers. observ.) and, with the exception of short foraging sorties and the reproductive wanderings of mature males, live their entire lives within a burrow (Wallace, 1942; McCrone, 1964; McQueen, 1978; Humphreys, 1975; pers. observ.). Generally, newly-dispersing spiderlings construct burrows in the vicinity of the maternal burrow (McQueen, 1978).

Methods and Materials

Specimens—I collected *Geolycosa micanopy* from Alachua, Levy, Marion and Putnam counties Florida during December 1982 and March 1983 and *G. turricola* from Oktibbeha County, Mississippi in March 1983. The spiders were housed at room temperature (21° C) and lighting (ca. 10:14 light:dark) in individual translucent plastic cups containing sand. Most of the spiders constructed burrows in the cups. The spider's diet consisted of crickets, wingless flies and tobacco budworm larvae (*Heliothis* sp.); and free water was provided.

Several spiders had mated before collection and constructed egg cases in the lab. Most females held the egg case until the young emerged and then tolerated them on her back until they dispersed. However, two *G. micanopy* and one *G. turricola* cast the cases from the burrows. The young from these cases were used in the experiments because their feeding experience could be closely controlled. Abandoned cases were kept in individual petri dishes. After about two weeks, I made a small opening in the egg sac and the young emerged. The number of young used for the study was 121 and 98 for the two *G. micanopy* egg cases and 119 for the *G. turricola* egg case. Spiderlings congregated on a cotton ball placed near the egg case. Each individual was placed into a glass vial within one week of emergence and held without food (water provided via cotton swab) for about two weeks, at which time the experiments began.

Experimental design and hypotheses—Three experiments were designed to test hypotheses concerning independence among dichotomous grouping variables arranged in three three-way

Table 1. Observed cell frequencies of burrow establishment for *Geolycosa turricola* and *G. micanopy* under experimental conditions. B = burrow established, NB = no burrow established.

	G. turricola				*G. micanopy*			
	Fed		Unfed		Fed		Unfed	
	B	NB	B	NB	B	NB	B	NB
Vegetation	25	4	13	17	23	8	7	24
No Vegetation	20	10	9	21	22	7	12	18
Crevice	—	—	—	—	19	6	20	4
No Crevice	—	—	—	—	16	9	13	11

contingency tables. The variables were chosen because of their possible importance as factors in burrow construction based on casual and quantitative observations of laboratory and field populations of five species of *Geolycosa* (*G. turricola, G. micanopy, G. patellonigra, G. ornatipes, G. hubbelli* and *G. escambiensis*). The variables were:

(1) Prey/no prey (PREY)—indicating whether food was provided during the experimental period.
(2) Vegetation/no vegetation (VEGETATION)—indicating whether small bits of grass were provided in the experiemental container.
(3) Crevice/no crevice (CREVICE)—indicating whether a depression in the burrowing surface was provided.
(4) Burrow/no burrow (BURROW)—the "dependent" variable, indicating whether a burrow was constructed. Any burrow which was large enough to contain the spider was scored as an established burrow.

For each experiment I tested two hypotheses concerning a three-way contingency table defined by the variables PREY, BURROW and one of the other two variables (Table 2). The experiments and anaylyses were performed for the two species separately for the data pertaining to the variable VEGETATION. No formal statistical comparison of the data for the two species was made. Analysis involving the variable CREVICE was carried out on *G. micanopy* only. The hypotheses were tested by Chi-square goodness-or-fit tests using Goodman's (1970) maximum likelihood estimators to obtain the expected cell frequencies.

Sand was used as the burrowing medium in all cases. Spiderlings which were to receive food were given newly-hatched crickets at the beginning of the experimental period. A metal probe was used to make small crevices in the sand where necessary. Restricted randomization was used to assign roughly equal numbers of spiderlings to treatment groups (fed, unfed, etc.). Specimens were held in their test containers at normal room temperature and light for a period of 36 h, at which time I observed whether each had established a burrow or not. Previous observations indicated that burrows are usually established within the first 24 h after dispersal.

Results

The first set of hypotheses tested the independence of burrowing with the variables VEGETATION and CREVICE respectively within the levels of the variable PREY (Table 2). The hypothesis that BURROWING is independent of VEGETATION within a PREY group (fed or unfed) was rejected for *G. turricola* but not for *G. micanopy* (Table 2). Both fed and unfed *G. turricola* showed a higher number of burrowers in the group that was provided with vegetation (86% and 43% burrowing in the fed and unfed groups respectively). For *G. micanopy,* the number of burrowers is approximately the same for the fed spiders with and without vegetation. A higher percentage of the unfed *G. micanopy* burrowed when no vegetation was present (23% and 40% for the group with and without vegetation respectively). More spiders burrowed in the presence of a crevice than when no crevice was available for both fed and unfed *G. micanopy.*

The second set of hypotheses tested the independence of BURROWING and PREY given the level of each of the other two variables. In every case, the hypothesis of independence was rejected (Table 2). In nearly every case, the percentage of spiderlings constructing burrows was lower in the unfed group. This is true for each level of the two variables, VEGETATION and CREVICE except for the unfed *G. micanopy* who were provided a crevice. In that case, more spiderlings constructed burrows than did not.

Discussion

The results indicate that, of those variables considered, PREY was most strongly associated with the establishment of a burrow. In nearly every case, groups of spiderlings which were given food had a

Table 2. Hypotheses and results of Chi-square goodness-of-fit tests. A = vegetation/no vegetation (i = 1,2...I); B = crevice/no crevice (i = 1,2...I); C = fed/unfed (j = 1,2...J); E = burrow/no burrow (k = 1,2...K); (see text for detailed explanation of variables A, B, C, and D). F_{ijk} = Maximum likelihood estimate of expected cell frequency (Goodman, 1970). f = marginal value for the superscripted variable for the appropriate subscripted row and/or column.

Hypothesis	F_{ijk}	df	*G. turricola* χ^2 p	*G. turricola* χ^2 p
a) D independent of A given C	$f_{ji}^{CA} \cdot f_{jk}^{CD} / f_j^C$	I(J–1)(K–1)	11.27 < .01	5.61 > 0.05
b) D independent of B given C	$f_{ji}^{CB} \cdot f_{jk}^{CD} / f_j^C$		---	38.47 < .01
c) D independent of C given A	$f_{ji}^{AC} \cdot f_{ik}^{AD} / f_i^A$	I(J–1)(K–1)	19.87 < .01	32.42 < .01
d) D independent of C given B	$f_{ij}^{BC} \cdot f_{ik}^{BD} / f_i^B$		---	15.10 < .01

higher percentage of burrows than those that were not. Although the experimental design allows consideration of only the importance of the presence of prey, higher rates of burrow establishment in the presence of food may imply either a nutritional advantage or a response to prey availability.

With respect to nutritional differences, even though burrowing behavior is innate and may be observed as early as in late pre-emergent spiderlings which have not fed (pers. observ.), the successful establishment of a burrow may be more likely if a spiderling is able to obtain food prior to dispersing. Many lycosid spiderlings disperse after only a short time on the mother (e.g., about seven days, Higashi and Rovner, 1975) and do not feed prior to dispersal (Foelix, 1982). My observations of field populations of other *Geolycosa* indicate that spiderlings may cling to the mother for up to three weeks and some young remain in the maternal burrow for at least one molt after leaving the mother's abdomen as Engelhardt (1964) found in *Trochosa* spp. A possible advantage of this extended association with the mother is that those spiderlings that remain may receive nurishment by sharing prey captured by the mother, as in *Sosippus floridanus* (Brach, 1976), or by cannibalism.

Hallander (1970) observed cannibalism in *Pardosa pullata* of the same brood, even in situations of high prey density. I held broods of *G. turricola* and *G. patellonigra* without food for six weeks and observed few instances of cannibalism. Cannibalism, therefore, is probably not a primary means of obtaining predispersal nourishment in *Geolycosa.* At present, I do not have information as to whether older juvenile *Geolycosa* that remain in the burrows are able to obtain food on their own. I have observed spiderlings clinging to the turret rim in a foraging position but I have never observed prey capture.

The means of obtaining predispersal nourishment (if such is obtained) notwithstanding, a lack of food per se does not preclude burrow construction. Significantly more burrows were constructed in the groups which were provided with food but many unfed spiderlings (average 40.8%) successfully constructed burrows. Also, observations of lab held and starved *G. patellonigra* indicated that burrowing may occur well after two weeks post emergence (pers. observ.).

Riechert and Luczack (1982) recently reviewed the literature concerning the selection of microhabitat in spiders. Environmental factors such as wind (e.g., Eberhard, 1971), vegetation structure (e.g., Enders, 1975) or temperature (e.g., Riechert and Tracy, 1975) and prey characteristics such as prey availability (e.g., Kronk and Riechert, 1979; Enders, 1977; Morse, 1981) are known to influence positioning of webs and the location of foraging sites in spiders. *Geolycosa* burrows function in both thermoregulation (Humphreys, 1975) and prey capture (Gertsch, 1942, pers. observ.), so the placement of the burrow may be related to these functions. However, the major thermoregulatory attribute of the burrow is its depth and not its location relative to the surrounding vegetation (Humphreys, 1975). *Geolycosa* regulate body temperature by moving up or down the tunnel. The selection of a burrow site, therefore, is more likely to be related to prey availability and microhabitat factors relating to ease of construction or which provide some protection from predators.

The results show a difference between *G. turricola* and *G. micanopy* in the relationship between vegetation availability and frequency of burrow establishment. Within a feeding state, the number of burrows established is independent of vegetation for *G. micanopy* but not for *G. turricola.* This difference reflects the turret construction habits of the two species. *Geolycosa turricola* nearly always constructs a conspicuous turret from whatever material is available, whereas *G. micanopy* shows considerable variation in turret construction and often has burrows with no turret (Wallace, 1942). The different relationship between burrowing frequency and vegetation is probably not a result of a preference for vegetation material used in the experiments, since there appears to be no specificity for turret material in *Geolycosa* (Wallace, 1942).

Nearly all *Geolycosa* observed in the lab readily used artificially constructed burrows. Field observations of dispersing *G. turricola* (Miller and Miller, in prep.) indicate that over one half of burrows constructed by dispersing *G. turricola* spiderlings were built within a surface crack or depression. The results presented here also indicate a preference for burrowing when a surface irregularity is present. Surface cracks and crevices could provide protection from predators and thermoregulatory advantage during the initial phase of

burrow construction. They may also give the spider a foraging advantage by providing an ambush location. Evidence of the importance of surface cracks is given by the unfed *G. micanopy* which were provided with cracks. That group constructed nearly as many burrows as the fed group.

Summary

The relationship between the establishment of a burrow and presence of prey, availability of vegetation and the presence of a crevice in the burrowing surface was investigated in newly-dispersing *Geolycosa turricola* (Treat) and *G. micanopy* Wallace. The establishment of a burrow by *G. turricola* was dependent on the presence of vegetation within a feeding group. Establishment of burrows by *G. micanopy* was dependent on the presence of a crevice (not tested for *G. turricola*). Burrow establishment was found to be dependent on prey availability for any level of the other variables. The dependence on vegetation for burrow establishment in *G. turricola* is attributed to a greater tendency to build turrets in that species. The higher burrowing frequency in the groups that received food during the experiment is thought to be related to nutrition and/or prey availability. The tendency to build new burrows in crevices is known from field studies and may be related to advantages of protection from predators, thermoregulation, or foraging position imparted by the crevice.

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RECENTLY RECOGNIZED TYPES OF SOME HOMOPTERA DESCRIBED BY DR. ASA FITCH[1]

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Dr. Asa Fitch (1809–1879) proposed 165 new species and subspecies names in the Homoptera. They are taxonomically distributed as follows: Cicadidae (2), Membracidae (21), Cicadellidae (34), Cercopidae (9), Delphacidae (2), Derbidae (7), Cixiidae (2), Achilidae (2), Issidae (2), Psyllidae (9), Aleyrodidae (1), Aphididae (52), Adelgidae (2), Phylloxeridae (4), Diaspididae (5), and Coccidae (11). He proposed the names in print from 1851 to 1872, mainly in his Homoptera catalogue (1851) and the *Transactions of the New York State Agricultural Society.*

Dr. Fitch never designated types for his new species and subspecies. However, he did label nearly all of his specimens with individual numbers. He recorded these numbers consecutively in four individual registers, along with collecting dates, localities, and other pertinent information. Label numbers in black ink written on white paper are recorded in one register of specimens from New York State. Label numbers in black ink crossed with one or two red lines and written on white paper are recorded in a second register of specimens from New York State. One red line indicates a number less than 10,000, and two red lines indicate a number to which 10,000 should be added. Label numbers in red ink written on white paper are recorded in a third register that lists specimens from elsewhere in North America. These three registers are in the possession of the New York State Museum. The fourth register, owned by the Museum of Science, successor to the Boston Society of Natural History, lists specimens from elsewhere in the world. The corresponding labels are written in black ink on colored papers. Dr. Fitch also kept individual sheets of notes on every species of which

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he was aware. If he had specimens of any one species, he recorded the specimen label numbers along with collection data on the appropriate manuscript sheet. Most of these notes are in the New York State Museum. Many of the Homoptera notes are in the Smithsonian Institution Archives and the files of the United States National Museum aphid collection.

According to the International Code of Zoological Nomenclature, the type series of a species or subspecies consists of all the specimens on which its author bases the species (Article 72b). The closest available approximation to a type series for a species or subspecies authored by Dr. Fitch consists of those specimens that can be proven, through a perusal of his registers and notes, to have been in his collection before or during the year in which the relevant species or subspecies name was first made available. In the introduction to his Homoptera catalogue, dated February 22, 1851, Dr. Fitch acknowledged the loan of all of Dr. Thaddeus William Harris's collection of Homoptera. In a letter to Dr. Harris, Dr. Fitch stated that he was forwarding copies of his Homoptera catalogue. He also stated that it would be a pleasure for him to add specimens from his collection to Dr. Harris's collection.[2] That letter is dated March 1–4, 1851.

The T. W. Harris insect collection at the Museum of Comparative Zoology, Harvard University, is segregated from the main collection. In it, several of Dr. Fitch's specimens are readily recognized by the label style and handwriting (Fig. 1). Some of these are specimens of species that Fitch described in his Homoptera catalogue. Those that were in Dr. Fitch's possession before February 28, 1851 (the earliest publication date for the Homoptera catalogue that can be demonstrated by evidence) can be considered types, but they have never been recognized as such. In most cases, these specimens are part of a syntype series, and other specimens can be found in the New York State Museum (McCabe and Johnson 1980) or the United States National Museum. In these cases, lectotypes should be designated if that has not already been done. Other specimens in the Harris collection are the only known extant specimens from the Fitch collection that Dr. Fitch considered to be representatives of certain species that he authored.

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[2]Fitch to Harris, 1–4 March, 1851; Museum of Comparative Zoology, Harvard University.

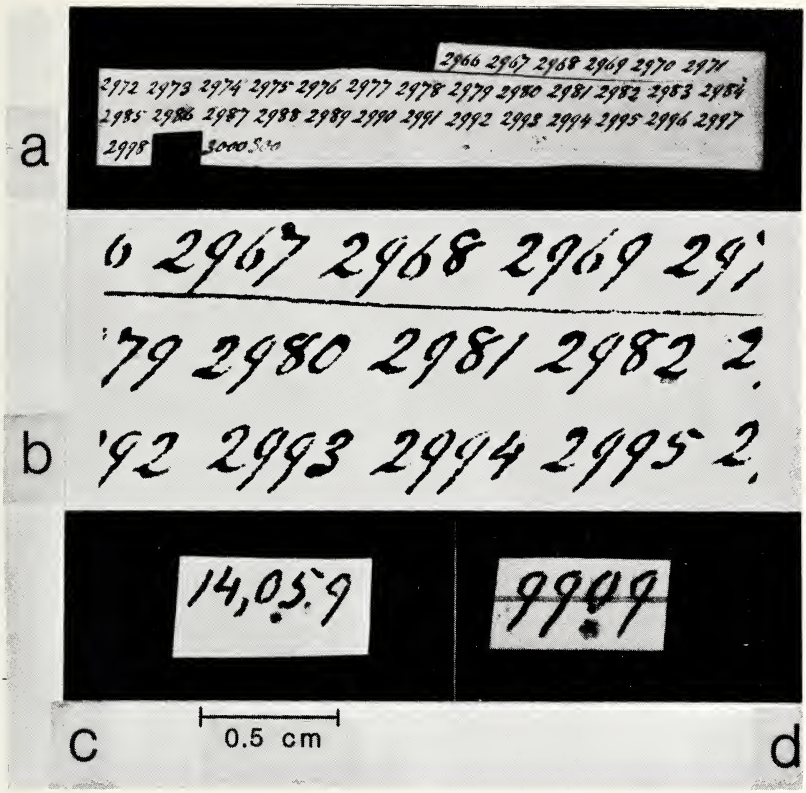

Fig. 1. Dr. Asa Fitch's handwriting and style of insect labels. a, uncut strip of labels; b, close-up view of a section of a; c, New York insect label 14,059, black ink on white paper; d, New York insect label *9909, black ink on white paper, crossed with one red line. Labels c and d same scale.

The following list contains brief descriptions of specimens from Dr. Fitch's collection that can now be found in the Harris collection. Generic and specific names are spelled exactly as they were in the original publications. Only specimens of species authored by Dr. Fitch are listed. The label numbers that are preceeded by one or two asterisks correspond with specimen labels that are written in black ink on white paper and crossed with one or two red lines, respectively. A summary of collecting data, derived from Dr. Fitch's registers and notes, accompanies each description of a specimen.

Membracidae

Uroxiphus caryae Fitch, 1851:52.
*3992, Greenwich, NY, 24.viii.1846.
*3997, Greenwich, NY, 24.viii.1846.
Tragopa dorsalis Fitch, 1851:52.
**134, Salem, NY, 25.vii.1851.
**137, Salem, NY, 25.vii.1851.
Cyrtoisa fenestrata Fitch, 1851:49.
*6927, Long Island, NY, 1847.

Cicadellidae

Idiocerus alternatus Fitch, 1851:59.
*8665, Salem, NY, 7.v.1851.
*8828, Salem, NY, 10.v.1851.
*9075, Salem, NY, 19.v.1851.
Helochara communis Fitch, 1851:56.
*8761, Salem, NY, 10.v.1851
Amblycephalus curtisii Fitch, 1851:61.
12,702, Salem, NY, 22.xi.1850.
Gypona flavilineata Fitch, 1851:57.
*6304, Salem, NY, 10.ix.1847.
Jassus fulvidorsum Fitch, 1851:62.
*6178, Salem, NY, 21.viii.1847.
Amblycephalus melsheimerii Fitch, 1851:61.
*4911, Salem, NY, 5.vii.1847.
Athysanus minor Fitch, 1851:60.
*4869, Salem, NY, 5.vii.1847.
Athysanus nigrinasi Fitch, 1851:61.
*2983, Jackson, NY, 16.vi.1846.
Aulacizes noveboracensis Fitch, 1851:56.
*9936, Salem, NY, 12.vii.1851.
Idiocerus pallidus Fitch, 1851:59.
*6059, Salem, NY, 19.viii.1847.
*9834, Salem, NY, 5.vii.1851.
Empoa querci Fitch, 1851:63.
13,299, Stillwater, NY, vii.1848.
Amblycephalus sayii Fitch, 1851:61.
*9234, Salem, NY, 30.v.1851.

Bythoscopus strobi Fitch, 1851:58.
*9397, Salem, NY, 5.vi.1851.
Erythroneura tricincta Fitch, 1851:63.
*6402, Salem, NY, 10.ix.1847.
Bythoscopus unicolor Fitch, 1851:58.
2021, Tullehassie, AR [Tullahasee, OK], viii.1851.
*4909, Salem, NY, 5.vii.1847.
Athysanus variabilis Fitch, 1851:60
*9822, Salem, NY, 5.vii.1851.
Pediopsis viridis Fitch, 1851:59.
*9836, Salem, NY, 5.vii.1851.
**153, Salem, NY, 25.vii.1851.
Erythroneura vulnerata Fitch, 1851:62.
*6467, Salem, NY, 10.ix.1847.
*6621, Greenwich, NY, 20.ix.1847.
*6629, Greenwich, NY, 20.ix.1847.

Cercopidae

Clastoptera testacea Fitch, 1851:53.
*5322, Salem, NY, 23.vii.1847.

Delphacidae

Delphax arvensis, 1851:46.
12,358, Salem, NY, 3.vi.1847.
Delphax dorsalis Fitch, 1851:46.
*8500, Salem, NY, 26.iv.1851.
*8578, Salem, NY, 29.iv.1851.

Cixiidae

Cixius pini Fitch, 1851:45.
474, Winhall, VT, 17.vi.1847.

Issidae

Bruchomorpha dorsata Fitch, 1857:396.
1555, Tullehassie, AR [Tullahassee, OK], 1.vi.1851.
Naso robertsonii Fitch, 1857:396.
1776, Tullehassie, AR [Tullahassee, OK], vii.1851.

PSYLLIDAE

Psylla carpini Fitch, 1851:64.
*9224, Salem, NY, 30.v.1851.

APHIDIDAE

Aphis crataegifoliae Fitch, 1851:66.
*9287, Salem, NY, 2.vi.1851.
Aphis populifoliae Fitch, 1851:66.
*9294, Salem, NY, 5.vi.1851.
*9298, Salem, NY, 5.vi.1851.
Eriosoma pyri Fitch, 1851:68.
*4053, Salem, NY, 10.xi.1846.
*4054, Salem, NY, 10.xi.1846.
Aphis rudbeckiae Fitch, 1851:66.
11,715, Salem, NY, 13.vii.1846.
11,717, Salem, NY, 13.vii.1846.

Dr. Fitch described six new genera, 85 new species, and five new subspecies in his Homoptera catalogue. The New York State Museum's collection still contains type specimens of 60 of the species and subspecies. The remainder have been considered destroyed (Lintner 1893, McCabe and Johnson 1980). The specimens that Dr. Fitch listed in his catalogue were numbered 609-874, and he tagged the specimens with numbered labels printed expressly for that purpose (Funkhouser 1915). These numbers bear no relationship to the numbers in Dr. Fitch's manuscript species notes or specimen registers. In the United States National Museum there are six specimens labelled in Dr. Fitch's handwriting with three digit numbers that correspond with those in his Homoptera catalogue. They are two specimens of Psyllidae, *Livia femoralis* Fitch (838) and *L. vernalis* Fitch (836), and four specimens of Aphididae, *Aphis betulaecolens* Fitch (848), *A. cerasicolens* Fitch (841), *A. berberidis* Fitch (842), and *A. sambucifoliae* Fitch (850). Specimen 842 is also labelled *Aphis pinicolens* Fitch, but not in Fitch's handwriting. A seventh specimen in the USNM—a specimen of *Aphis cornifoliae* Fitch—is labelled "846 Fitch," "Type," and "Female," corresponding with the information given in Fitch's catalogue, but these labels are not in Fitch's handwriting. Two more specimens of Aphididae, *Lachnus abietis* Fitch (854) and *L. alnifoliae* Fitch (857),

are described in Smith and Parron's list of North American Aphididae (1978) as "nearly destroyed, in USNM," but I have been unable to locate them.

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PRODUCTION AND USE OF SECRETIONS PASSED BY MALES AT COPULATION IN *PIERIS PROTODICE* (LEPIDOPTERA, PIERIDAE)*

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Introduction

During copulation in many species of insects the male passes to the female sizeable quantities of accessory gland secretions with the sperm (Thornhill and Alcock, 1983). Recently it has been shown in the Lepidoptera that these secretions may represent a nutrient investment by the male that is used by the female in the production of eggs and in somatic maintenance (Boggs and Gilbert, 1979; Boggs, 1981; Boggs and Watt, 1981; Goss, 1977; Greenfield, 1982). Typically these secretions are contained within a spermatophore with the sperm or they may be passed as loose secretion. The perspective that these secretions may constitute a nutrient investment by males has some important implications for how male and female lepidopterans should behave (Marshall, 1982; Rutowski, 1982; see also, Gwynne, 1982).

In spite of recent interest in these secretions there are few studies of the patterns of their production and use within and between species of Lepidoptera (e.g., Boggs, 1981; Greenfield, 1982; Rutowski et al., 1983). This paper reports data on patterns of variation in the quantity of material passed to females during copulation by males of the checkered white butterfly (*Pieris protodice* Boisduval and LeConte) and the disappearance of these secretions from the female's reproductive tract. The secretions are received by the female in the bursa copulatrix which in this butterfly species is composed of two sacs, the corpus bursa and the appendix bursa. These are connected in series with the appendix bursa being furthest from the copulatory opening. During copulation the appendix bursa is filled with a whitish fluid and the corpus bursa is filled with

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a spermatophore that is formed within the bursa during copulation and contains sperm and secretions.

Methods and Materials

All observations were made at the Arizona State University Farm Laboratory from March to July in 1983. Here the butterflies use cultivated alfalfa as a nectar source and feral and cultivated crucifers as oviposition sites and larval foodplants.All hand-reared adults were grown from eggs collected in the laboratory or from young larvae collected in the field. In the laboratory larvae were reared either on broccoli (*Brassica* spp.) leaves or on cuttings of *Sisymbrium irio* L. in plastic shoe boxes under variable and uncontrolled conditions of light and humidity. The temperature in the laboratory was about 24° C.

Production of secretions during copulation

To examine the patterns of production of secretions by males, virgin females were released next to free-flying males and permitted to copulate with them. If the copulation lasted 60 min or less, both members of the pair were freeze-killed after the pair separated. Longer copulations were thought to indicate dysfunction or recent mating by the male. Males in the mated pairs were assessed with respect to wing wear (age), forewing length, and body weight (to the nearest 0.1 mg) (for techniques, see Rutowski et al., 1983). Females were assessed with respect to forewing length and the volume and wet mass of material received from the male during copulation (for technique see Rutowski et al. 1983). In some cases males were weighed and measured without killing so that they could be held overnight (without food and water) and returned to the field the following day to observe their performance in second matings. Male precopulatory body mass was estimated by adding the mass of the secretions imparted to his postcopulatory mass.

To examine the rate of use of the material received during copulation virgin females were mated to free-flying males as above and then held in cylindrical screen cages (9 cm diameter, 12 cm deep) in the laboratory under flourescent illumination. At various times after mating females were freeze killed and dissected to examine the material remaining in the bursa copulatrix. Sprigs of *S. irio* for oviposition and sugar water for food were available in these cages.

All summary statistics are given as mean ± standard deviation. The 0.05 level was used in all evaluations of statistical significance.

Results

Production of secretions by males

Various aspects of the observed copulations and the individuals that participated in them are summarized in Table 1. Again, all these copulations were less than 60 min in duration. All males were in fresh or only slightly worn condition. Several significant positive correlations reflect concordance in the measuring techniques. Male forewing length was significantly positively correlated with the estimate of male precopulatory body mass (Fig. 1A; $r=0.71$, $n=26$, $p<10^{-5}$) and a similar relationship was found between the volume and the mass of male-imparted secretions (Fig. 1B; $r=0.879$, $n=28$, $p<10^{-9}$).

Qualitative microscopic observations were made on squash mounts of material removed from the spermatophore and the appendix bursa found in 3 females. These observations suggest that the sperm packet is (1) discrete from the non-sperm matieral, (2) last to be deposited in the bursa copulatrix (closest to the bursal entrance), and (3) typically consititues 10% or less of the volume of material passed by the male.

On average males passed almost 8% of their precopulatory body mass at copulation. However, the quantity of material passed measured by volume or mass was not significantly correlated with either male forewing length (vs. volume: $r=-0.054$, $n=28$, $p=0.39$; vs. mass: $r=-0.108$, $n=28$, $p=0.29$) or male precopulatory body mass (vs. volume: $r=-0.095$, $n=26$, $p=0.32$; vs. mass: $r=0.0066$, $n=26$, $p=0.48$). The percent of male precopulatory body mass passed at copulation was significantly negatively correlated with both measures of male size (Fig. 2; forewing length: $r=-0.625$, $n=26$, $p=0.0003$; precopulatory body mass: $r=-0.654$, $n=26$, $p=0.0001$). These results suggest that all males regardless of size pass a typical amount of material. Small males must then obviously pass a larger proportion of their body mass to achieve this typical quantity.

Copulation duration was not significantly correlated with the volume of material passed ($r=-0.243$, $n=26$, $p=0.115$) but was significantly negatively correlated with the mass of secretions passed by males (Fig. 3; $r=-0.34$, $n=26$, $p=0.045$). There may be a

Table 1. Summary of 28 copulations that lasted 60 min or less.

Variable (units)	Mean	Standard deviation	Sample size	Range
Male forewing length (mm)	23.9	1.1	28	21–26
Estimate of male precopulatory body mass (mg)	52.9	10.9	26	29.1–70
Female forewing length (mm)	23.3	1.49	28	19–26
Copulation duration (min)	31.7	9.23	26	22–60
Volume of male-imparted secretions (μ)	3.44	1.08	28	1.36–5.46
Mass of male-imparted secretions (mg)	3.89	1.15	28	1.78–5.9
% of male body mass passed	7.88	2.59	26	2.7–12.7

tendency in copulations lasting an hour or less for females to receive smaller quantities of material than in long copulations.

Female forewing length was not significantly correlated with male forewing length ($r=-0.0404$, $n=28$, $p=0.42$) which suggests size assortative mating does not occur in this species. Female forewing length was not significantly correlated with the volume of secretions received ($r=-0.25$, $n=28$, $p=0.10$) or the mass of secretions received ($r=0.228$, $n=26$, $p=0.122$). Female size apparently does not influence the quantity of material passed.

Ten males were mated and then successfully remated 24 hours later. Table 2 summarizes a comparison of first and second matings by these males. Statistical comparisons reveal that significantly less material was passed in the second matings ($t=4.32$, 9 df, $p<0.002$) and males passed a significantly smaller proportion of their body mass ($t=3.3$, 9 df, $p<0.01$). Although not all copulation durations were precisely measured, those that were displayed no difference between the durations of first and second matings separated by 24 hrs ($t=0.107$, 15 df, $p=0.46$).

Rate of use of male secretions by female

Fig. 4 shows the mass of material remaining in the females's reproductive tract at various times after mating. During the first day or two after copulation little material has left the bursa copulatrix but then the decline is rapid until day 5 at which point it seems to level off. The correlation between days since copulation and material left in the bursa copulatrix was negative and highly significant ($r=-0.751$, $n=46$, $p<10^{-8}$).

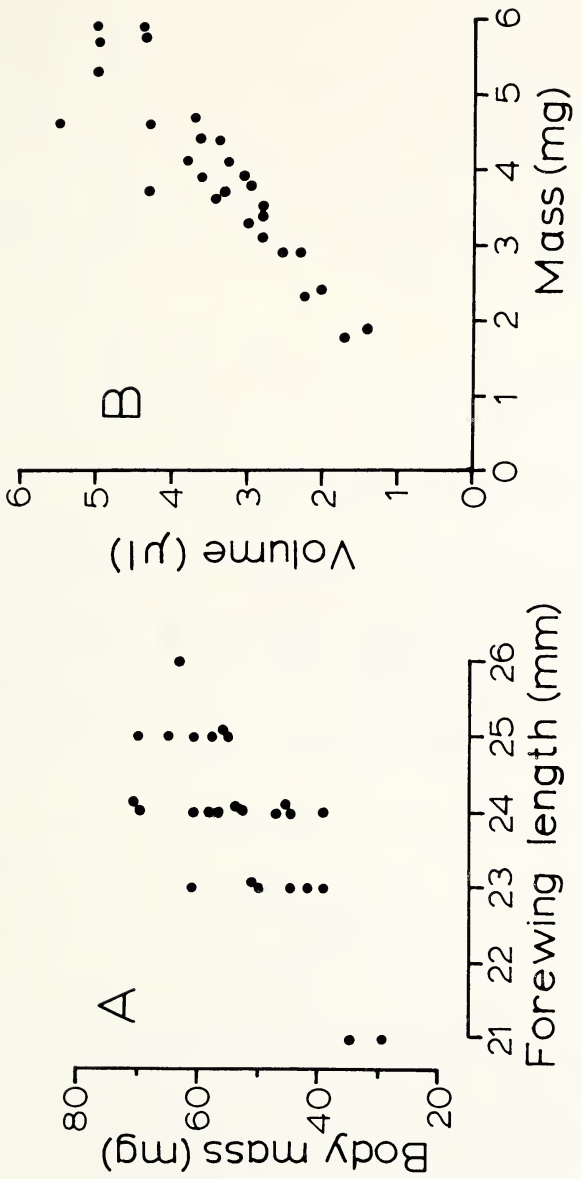

Figure 1. Concordance in measures of (A) male size and (B) quantity of material passed at copulation.

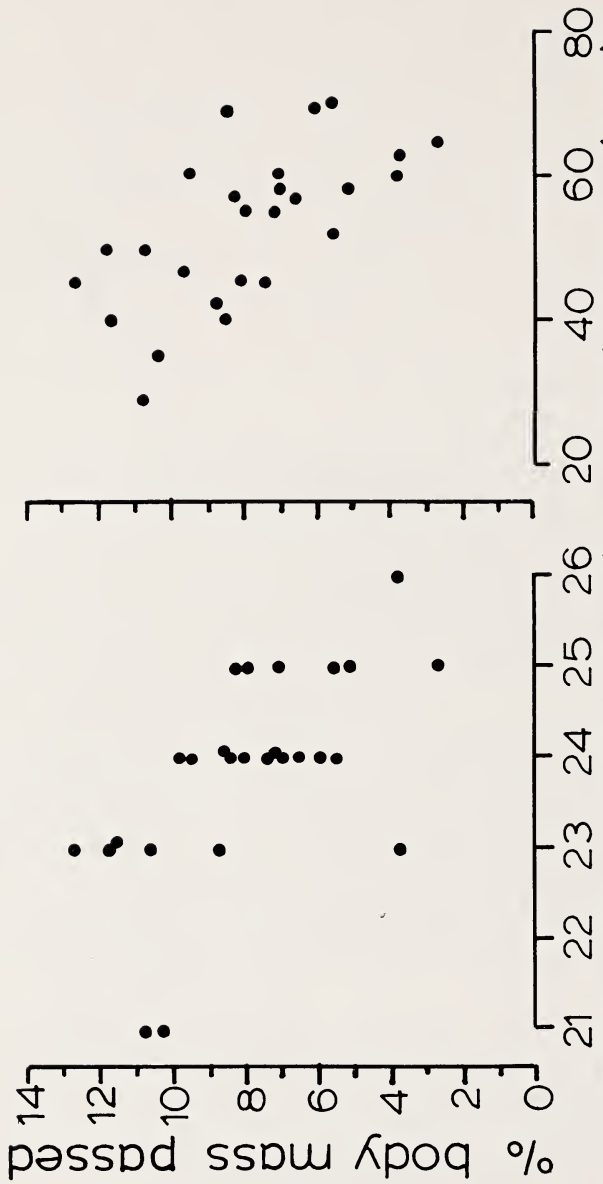

Figure 2. The relationship between the percentage of male body mass passed at copulation and (left) the male's forewing length and (right) his precopulatory body mass.

The conditions under which these females were kept in the laboratory were admittedly highly artificial and restricted the females's movements. As a result oviposition behavior was erratic but several major trends were apparent. No female oviposited before day two after copulation. Hence, depletion of the secretions begins at the same time as the production of eggs. The maximum number of eggs produced by any female was 114. The number of eggs produced was not significantly positively correlated with the number of days since copulation ($r=0.306$, $n=25$, $p=0.07$). No female laid infertile eggs regardless of time since mating and number of eggs laid.

Observations on field-caught females

Seventy-three females were collected in the field during this study for examination of the contents of their reproductive tracts. Of these only one was a virgin, 56 carried one spermatophore, and 15 carried two spermatophores meaning they had mated twice. The likelihood of a female mating twice increased with age as indicated by wing wear. Of 30 fresh females 10% were twice mated while of 41 females that showed noticeable wing wear 29% were twice mated ($\chi^2=3.86$, 2 df, $p<0.05$). In 9 of the twice mated females it was evident that the female only remated when the spermatophore from the first mating was in a greatly depleted state. In these females, the spermatophore furthest from the entrace to the bursa copulatrix was collapsed and clear in color while the other had its neck or collum extending into the ductus bursa and was full, white, and round.

Discussion

Production of secretions by males

Males of *P. protodice* pass on average 7–8% of their body mass at a single copulation. This figure is in the range of values observed in a variety of butterflies by Rutowski et al. (1983). Moreover, the courtship behavior of *Pieris protodice* follows the basic pattern observed in other butterflies: the male approaches the female, the female alights, the male buffets the female briefly with his wings, the male alights and couples with the female (Rutowski, 1979a). These data support the hypothesis of Rutowski et al. (1983) that a lack of interspecific diversity in the overall complexity of butterfly courtship behavior is paralleled by a lack of variation between species in the proportion of male body mass passed at copulation.

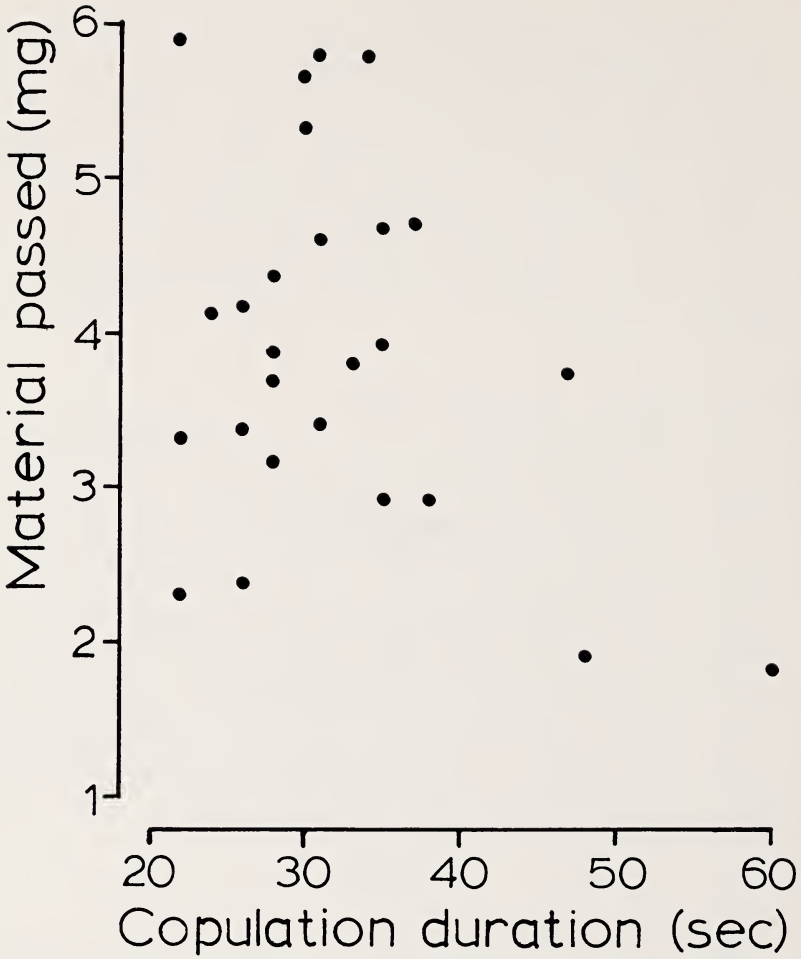

Figure 3. The relationship between the mass of material passed by a male at copulation and the duration of copulation.

The quantity of material passed by a male was not related to his size, contrary to observations made by Boggs (1981) on a heliconiine butterfly, Greenfield (1982) on a pyralid moth, and Gwynne (1982) on a katydid. However, males, independent of size, produce a typical quantity of material during a copulation and the proportion of a male's body mass passed varies inversely with male size. Because of the critical role inflation of the bursa copulatrix plays in

Table 2. A comparison of the performance of males in matings separated by 24 hours. See text for details.

	First copulation			Second copulation		
Parameter (units)	X±SD	N	Range	X±SD	N	Range
Copulation duration (min)	33.2±11.8	10	22–60	32.6±10.8	7	23–54
Mass of material passed (mg)	4.47±1.44	10	1.78–5.9	2.37±0.504	12	1.45–3.12
% of male body mass passed	8.8±1.95	10	2.75–12.7	5.88±0.898	10	4.7–6.95
Volume of material corpus bursa (μ)	3.63±0.997	10	1.56–4.6	1.85±0.411	12	1.18–2.52

stimulating female refractoriness to courtship immediately after mating (Sugawara 1979) selection must favor males that produce a quantity of material that will cause most females to be unreceptive after mating. Sperm precedence has been shown in another pierid (Boggs and Watt, 1981) so stimulating female refractoriness will help protect a male's investment from exploitation by other males.

The lack of a relationship between male size and the absolute quantity of material a male is likely to pass may help understand the observation that very few unsuccessful courtships were observed during this study or in another (Rutowski, 1979a) that were lengthy and thereby suggested termination by the female. This is in contrast to recent observations on *Colias eurytheme* Boisduval in which almost half of all observed unsuccessful courtships were apparently female-terminated (Rutowski, unpublished data). In *P. protodice* choice by females on the basis of size among males may not yield significant material benefits. In a pyralid moth (*Plodia interpunctella*), Greenfield (1982) found that male size was proportional to mating success and that large males passed larger quantities of material. However, female egg output was not related to the size of her mate.

In a previous study of *P. protodice,* males in copulations separated by an average of only 10 min produced one quarter of the material in the second copulation that they produced in the first (Rutowski, 1979b). In that study the quantity of material passed was assessed only by estimating the volume of secretions passed into the spermatophore. Similar assessments are given in this study for first

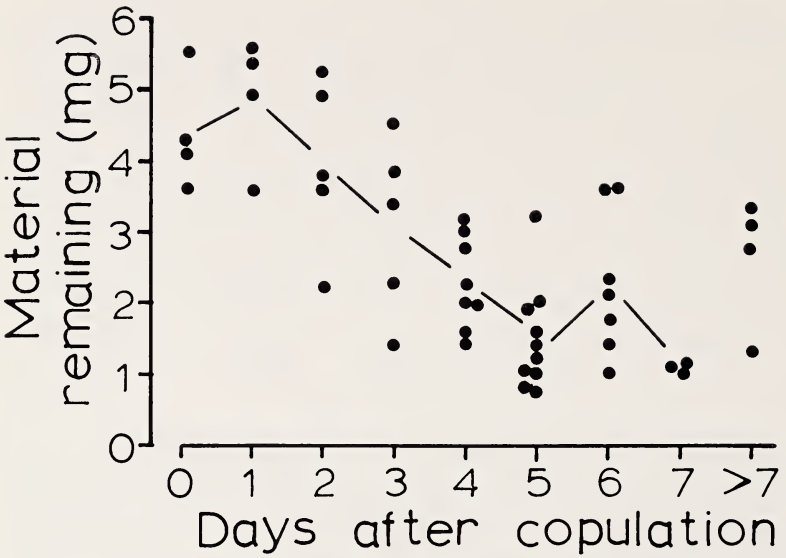

Figure 4. The quantity of material remaining in the female's bursa copulatrix as a function of the time since copulation. Line shows change in mean values for days 0 through 7.

and second matings separated by 24 hrs (Table 2). Several comparisons are valuable here. First, there was no significant difference between the amount of material passed in first copulations in 1979 and 1983 ($t=0.614$, 26 df, $0=0.27$). In addition, males passed significantly more material 24 hrs after the first mating than they did 10 min after the first mating ($t=2.95$, 17 df, $p=0.004$). These comparisons point out the consistency in the observations between the two years and more importantly that while copulation durations indicate that males have substantially recovered in 24 hr their supply is still somewhat depleted. However, this depletion may be a result of housing males between matings without food and water. In fact most of these males flew immediately to nectar sources upon release in the field. There is much to be learned about the performance of males in third matings and their performance in second matings when they have access to nectar.

Use of secretions by females

The rate at which females deplete the secretions they have received from males is greatest between the second and fifth days

after mating. This suggests that a female's supply of secretions but not sperm is effectively depleted beginning at about six days after mating. Suzuki (1979) examined the phenomenon of multiple mating in *Pieris rapae* L., a close relative of *P. protodice,* and found that most females mate for the second time about 6 to 8 days after being released as a virgin in the field. These data support Suzuki's hypothesis that *Pieris* females may multiply mate to gain nutrients in that they appear to be doing so at a time when their supply of secretions from previous matings is largely depleted. This hypothesis is also confirmed by the data from the dissections of field-collected females in which at least one of the spermatophores carried by twice-mated females was often small and greatly depleted.

Summary

This study examines the production and use of secretions passed by a male during copulation to a female in the checkered white butterfly (*Pieris protodice*). Males pass about 7 to 8 percent of their body weight at copulation in the form of secretions deposited in the female's reproductive tract. No correlation between the quantity of material passed and male size was found. However, it was found that the proportion of male body mass passed was inversely correlated with body mass suggesting that all males, regardless of size pass a typical quantity of material. A mating depletes the material a male has for subsequent mating but only temporarily. Males were found to have mostly recovered their potency in 24 hrs, even without food or water between matings.

Females have mostly depleted the material received from males in about 5 to 7 days. In the field females carrying multiple spermatophores always had one that was greatly depleted indicating that they remate only when material from a previous mating was depleted. The results are compared to information on the use and production of male-imparted secretions and mating behavior in other butterflies.

Acknowledgements

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FEMALE MONOGAMY AND MALE COMPETITION IN *PHOTINUS COLLUSTRANS* (COLEOPTERA: LAMPYRIDAE)*

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Introduction

Matings by *Photinus collustrans* females can easily be kept track of in the field. These brachypterous females live in burrows and remain near them. About 20 minutes after sunset males start to fly and search for females, which take positions on the soil surface or on vegetation (Lloyd 1966). Females flash in response to the signals of flying males, which locate them by their responses. Each night sexual activity is restricted to a period about 18 minutes long (Lloyd 1966; also see T. Walker 1983 for a discussion of such 'sprees'). *P. collustrans* females live about 10 days after their first appearance (Wing 1982); by observing a female for about 20 minutes per night for 10 nights, every sexual activity of her life can be recorded. There is no evidence that females mate under circumstances other than those mentioned above.

This field study shows that only a very small proportion of *collustrans* females mate more than once. Yet the potential for female multiple mating apparently is the basis for the evolution of a complex of tactics used by competing males.

Methods and Materials

Field studies of *collustrans* were conducted in Alachua County, Florida. The site was a grassy area under scattered oaks, pines, and shrubs. The grass was mowed periodically. Two streetlights illuminated parts of the site.

Females were located by their flash and/or glow responses to penlight simulations of male mating signals (see Lloyd 1966). The location of each female was marked by placing a numbered flag about 15 cm to the north of her. Flags were 10 × 40 cm strips of

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plastic held in place with nails. Females use the same burrow throughout their adult lives[1] (Wing 1982), and numbered flags placed at the burrow location were sufficient to identify each individual. Copulations were timed with a stopwatch, and some were observed with a magnifying glass.

An 18 × 20 m area was searched for females nightly starting before male flights began and ending after they had ended for the night. The location of each female was marked and I inspected her position at approximately 1 min intervals.

Each time a female's position was visited on a given night, she was presented penlight simulations of the male signal. Because females do not respond following a successful mating, but pause and then re-enter their burrow (Wing 1982), a female answer to my signal indicated that she was not yet mated. If she failed to respond, I determined whether she was 1) still out but not responsive; 2) mating; 3) entering her burrow; or 4) gone. All female locations were checked until the adult season was over.

Because the same area was searched nightly throughout the season, when a new female appeared she was almost certainly a virgin making her first appearance. Complete sexual histories of 108 *collustrans* females were recorded.

Results

Of the 108 females whose complete sexual histories were determined, 104 mated only once. The general sexual pattern was as follows. The female appeared by her burrow nightly until she attracted a male ($\bar{x} = 2$ nights). The male, having located the female by her continued responses to his signals, landed nearby and walked to her. Upon making physical contact, the male climbed upon the female, and copulated with her in the male-above position (Fig. 1). Copulation lasted about 1 min (details below). The male broke the connection, dismounted, and flew away leaving the female outside her burrow. Following copulation the female paused for seconds or minutes, and did not flash responses to signals of passing males. She then entered her burrow.

[1]During this study 91 females were individually marked with Tech Pen Ink dispensed from Hamilton's paint pots (T. Walker and Wineriter 1981). Females appeared for up to 10 consecutive nights. Every appearance by each marked female occurred at her original position.

Four females mated more than once. One of these females was dug from her burrow by a male, one was mated by a "sneaky" male, and two made themselves available to males by their own behavior.

The two repeated matings due to female behavior occurred when females mated and entered their burrows, but on subsequent nights left their burrows, responded to male signals, and mated again. Only three of 108 females appeared on nights subsequent to the first mating. Two mated again; one remated once, the other twice.

When more than one male landed at a responding female, the first male to reach her mounted and began copulation. The rival male attempted to mount the female (sometimes backwards), and to break the pair apart (Fig. 2). As a result, the copulating male moved or was pushed off the female and copulations proceeded in the tail-to-tail position, and variations thereof. (In the tail-to-tail position the male and female face in opposite directions while maintaining genitalic connection. Due to disturbance by rival males, pairs were sometimes moved into odd positions, even with the female on the copulating male's dorsum.)

Copulations were significantly longer when rival males were present. Mean duration for single male copulations was 57 sec (n=23, range 30–185 sec) compared to 842 sec (n=5, range 339–1410 sec) Mann-Whitney (U=115) $P < .0005$ when rivals were present. In these cases, copulating males maintained the genital connection until *after* the females had entered their burrow (Fig. 3). Females entered head first, dragging the coupled males backwards down the burrow. In one case, only the head and thorax of the male remained outside the burrow when the genital connection was broken. After disengaging, males climbed out and flew away. After the mated male departed, in four of seven cases the rival male tried to remove the female from her burrow. Rival males located the burrow opening by antennating the soil. Rivals dug at the burrow (Fig. 4), sometimes completely entering it. On one occasion the male succeeded in removing the female from her burrow and mated with her (this accounted for the third multiple mating) (Fig. 5). Unsuccessful males dug for as long as 35 min before leaving.

The fourth repeated mating resulted from another behavior of rival males and was observed once during this study and once since then. The rival "sneaky" male was non-aggressive, and made only occasional contact with the copulating pair. The rival gently antennated the pair and then walked away, returned and antennated

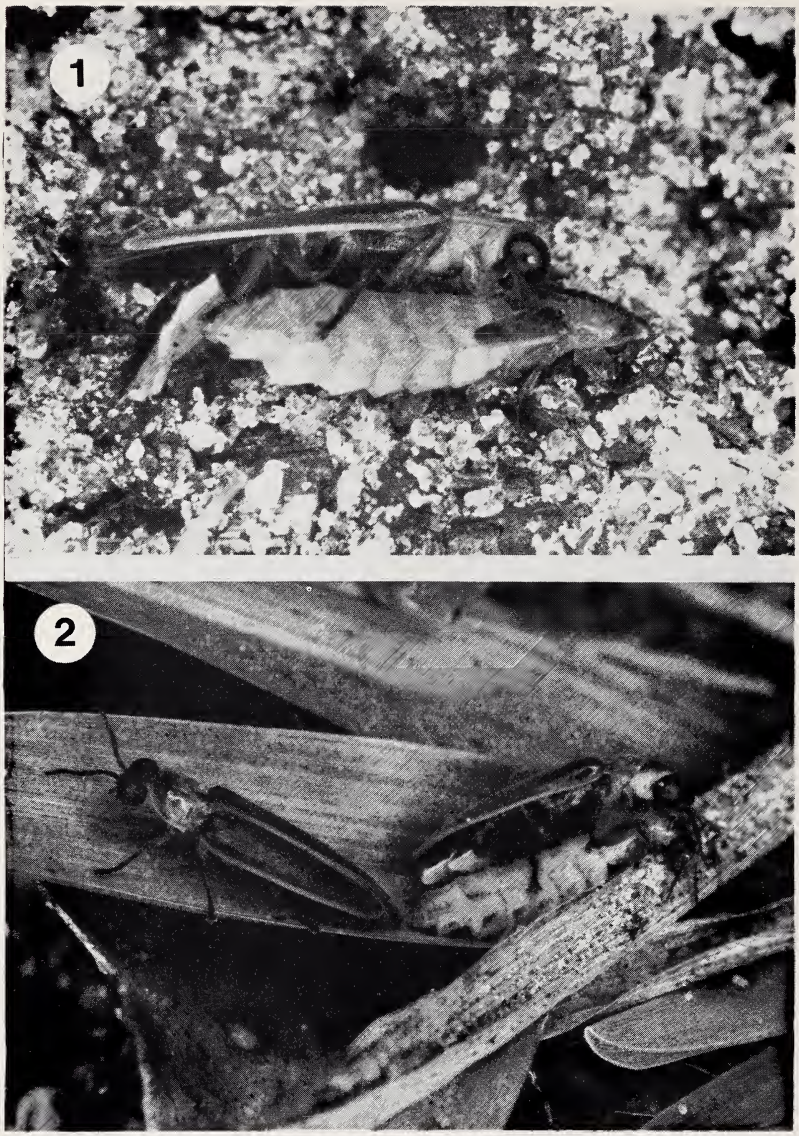

Fig. 1. *Photinus collustrans* male (above) mounting female. Note burrow opening in background. The female is about 11 mm long. Fig. 2. *Photinus collustrans* trio. Male on left is copulating. Rival has mounted female.

Fig. 3. Rival male (left) remains mounted as female enters burrow. Male on right is copulating. Fig. 4. Rival male digs at female's burrow.

again. The copulating male stayed in the male-above position, and copulation was not prolonged. After copulation, the male dismounted and flew away, leaving the female outside her burrow. The rival male then located the female and mated with her.

Discussion

Females are difficult for males to locate (Lloyd 1979). With a period of only about 18 min nightly to operate in, the usual male strategy after finding a female is to mate and, within a minute or so, return to the air searching for another female.

Females pause after mating, but do not answer the flashes of passing males. They then enter the burrow. Less than 3% of the females that mated ever made themselves available to males again (also see Wiklund 1982), and those that did may have had some fault in the mechanism that indicates whether sufficient sperm was acquired (also see W. Walker 1980).

During the pause before re-entering the burrow females are susceptible to another mating if found. Even after re-entering the burrow a female may be dug up and remated. Generally, then, if a male can gain physical access to a female, he can mate with her. The fact that an accessible female could be mated if found has led to prolonged copulation when a rival male is present (Parker 1970). Copulating males make the female physically unavailable by occupying her until she has returned to her burrow (see Sivinski 1983). Rival males try to break the coupled pair apart and attempt to gain access to the female by digging her from the burrow. The "sneaky" rival avoids triggering mate-guarding by the coupled male, and thereby gains access to the female after her first mate leaves.

The frequency of male encounters with rivals might vary with male density, but the overall proportion of females that mate repeatedly is probably rarely if ever much greater than the four per hundred found in this study.[2] The complex of male strategies and counter-strategies shown here reflects how important the potential for female multiple mating can be, even when only a small proportion of females actually mate more than once.

[2]Based on 71 matings observed when male density was at a 3-year peak (Wing unpublished data). It should also be noted that mated females are sometimes flooded from their burrows, and may remate under these circumstances (Wing 1982 and unpublished).

Fig. 5. Rival male pulls female from her burrow.

Summary

Four of 108 *Photinus collustrans* females mated more than once. One was dug from her burrow by a male, one was mated by a "sneaky" male, and two made themselves available to males after mating.

Acknowledgments

The photograph for Fig. 2 was made by T. G. Forrest. J. E. Lloyd introduced me to fireflies and reviewed the manuscript several times. Reviews by T. G. Forrest and J. Sivinski also improved the paper. Special thanks for comments by members of the Editorial Board at *Psyche*. Barbara Hollien typed the manuscript. S. A. Wineriter helped mount the photographs. Some of the work was funded by NSF grant no. DEB-7821744. Florida Agricultural Experiment Station Journal Series No. 4934.

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NON-DIAPAUSE OVERWINTERING BY *PIERIS RAPAE* (LEPIDOPTERA: PIERIDAE) AND *PAPILIO ZELICAON* (LEPIDOPTERA: PAPILIONIDAE) IN CALIFORNIA: ADAPTIVENESS OF TYPE III DIAPAUSE-INDUCTION CURVES*

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Diapause is generally regarded as a physiological adaptation which increases the probability of surviving the adverse season, and thus of reproducing after it is over. Many insect species show geographic differences in the environmental regimes which induce or inhibit diapause (e.g., critical photoperiod) and in the strength of the diapause induced. Such interpopulational differences are commonly viewed as "fine tuning" to local climates, accomplished by natural selection and reflecting a genetic basis (e.g., Istock, 1981). Intrapopulational differences in photoperiodic sensitivity and diapause strength (e.g., chilling requirement) also occur, and have been interpreted as polymorphisms which "spread the risk" of environmental uncertainty over the population (cf. Bradshaw 1973, Shapiro 1979, 1980a). In multivoltine insects in seasonal climates, offspring produced by the last seasonal generation of adults are commonly induced to enter diapause by specific combinations of environmental factors; in mid-latitudes these are likely to be decreasing photophase/increasing scotophase and decreasing or consistently low night temperatures. Warmer nights tend to shorten the critical photoperiod for a given population, or may effectively inhibit diapause altogether under field conditions.

Beck (1980) characterized diapause induction as falling into four response types. Type I is the common long-day response, in which long days inhibit diapause and there is a single threshold beyond which diapause occurs. Type II, the short-day response, is the reciprocal of Type I. Type III has two well-defined critical daylengths, such that diapause is induced between, say, 8 and 14 hours

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light, and inhibited when either less than 8 or more than 14 hr of light occur. Type IV is its reciprocal, in which diapause is inhibited over a relatively narrow range and induced both above and below. Of the four types, Type I is by far the commonest in temperate-latitude insects and Type IV the rarest. Low-latitude insects have rarely been examined for photoperiodic responses, though the different patterns of seasonality in low latitudes might be expected to produce a rather different picture than that seen in temperate zones.

Type III curves are known from a variety of insects. Among Lepidopterans, two important species that show them are the European Corn Borer, *Ostrinia nubilalis* (Hbn.) (Beck, 1962) and the Large White, *Pieris brassicae* L. (Danilevskii, 1961). The adaptive significance of the short-day threshold is unclear. Normally the entire population would have been induced by day-length-temperature interaction to enter diapause before the inhibition threshold was reached. Thus, the photosensitive stages would never be exposed to such short photoperiods in nature, and the existence of a short-day threshold would seem nonadaptive. This paper reports a situation in which Type III curves were demonstrably adaptive for two multivoltine Lepidopterans in nature.

The Systems

Papilio zelicaon Lucas and *Pieris rapae* L. are very common, widespread multivoltine butterflies in lowland California. Both have been monitored phenologically for up to 13 yr along a transect parallel to Interstate Highway 80 from sea level at the Suisun Marsh, Solano County, to treeline in the Sierra Nevada. We are concerned here with the phenology of populations at low elevations between the San Francisco Bay area and Sacramento. The flight seasons for both species may reach ten months (Table 1), with four (*P. zelicaon*) to about six (*P. rapae*) generations per year. Both species have facultative pupal diapause under conventional photoperiod-temperature control (Sims, 1980; Shapiro, unpublished data); both have Type III diapause-induction curves. Diapause is irreversibly determined no later than the fourth instar. *P. zelicaon* is the stronger diapauser and is unrecorded at any of our sampling sites between 1 December and 18 February. In some years the period with no *rapae* flying may, however, be as short as four weeks.

Table 1. Dates of first and last observed flights of two common multivoltine butterflies in lowland north-central California, based on standardized methodology and level of effort.

	Pieris rapae				*Papilio zelicaon*		
	Davis-Sacramento area[1]		Suisun Marsh[2]		Davis-Sacramento[1]	Suisun Marsh[2]	
	First	Last	First	Last	First[3]	First	Last
1972	ii.26	xi.29	--	x.21	iii.5	--	xi.5
1973	i.20	xii.24	--	xii.29	iii.14	iii.18	xi.18
1974	ii.1	xii.15	ii.2	xi.25	iii.19	ii.23	x.26
1975	ii.16	xii.5	i.30	xi.13	iv.11	iii.5	x.15
1976	i.25	xii.20	ii.15	xi.21	iii.10	iii.9	x.16
1977	--	xii.23	--	x.31	iii.6	iii.5	x.14
1978	ii.18	xii.2	ii.14	xi.15	iii.18	iii.10	x.11
1979	ii.17	xi.9	iii.5	xii.1	iii.31	iii.23	x.7
1980	ii.10	xi.26	--	xi.23	iii.28	iii.9	ix.28
1981	ii.14	xii.16	ii.21	xi.7	ii.22	iii.10	x.18
1982	ii.2	xii.19	ii.17	x.23	iii.20	iii.19	x.23
1983	ii.13	xii.18	iii.4	xii.17	iii.11	iii.14	x.23
1984	i.28		i.29		iii.6	iii.4	

Notes: [1]Consists of several study sites in Yolo and Sacramento Counties, all below 40m elevation.
[2]Near Fairfield, Solano County, at sea level.
[3]Last flight data not given for inland populations because numbers are usually very low late in the season as compared to near-coastal populations.

In contrast, the Pierid *Colias eurytheme* Bdv., which overwinters as a quiescent (non-diapausing) larva, flew continuously during the drought years of 1975–76 and 1976–77 and nearly so in 1983–84. Collections of mature larvae of both *P. zelicaon* and *P. rapae* made in late October and November over 12 yr have consistently given from 85–100% diapause pupae. Larvae of *P. zelicaon* are normally absent from all sites by the third week of November. *Rapae* larvae are occasionally found on garden cabbages and weedy Crucifers into early January. A fifth-instar larva was collected on a weed on 29 January 1979.

The winter of 1982–83 produced 200% or more of normal rainfall over most of northern and central California. Nearly 20 cm of rain fell in March 1983 at our study sites, and the weather remained showery and unsettled into May. The spring flights of most butterflies were late and poor; for many species the densities observed were the lowest in 12 yr. Both *P. rapae* and *P. zelicaon* were severely depressed at most sites; *P. rapae* was actually rare in spring, and the Willow Slough population of *P. zelicaon,* north of Davis, went extinct overwinter. The summer was unusually cool, cloudy, and moist. By autumn the populations of both species were near normal levels and at the Suisun Marsh *P. zelicaon* was commoner than usual at the end of the season. The latest flight recorded at Suisun for this species is 18 November (1973), a "false brood." Although the species shut down nearly a month earlier in 1983, the autumn brood oviposited three to four weeks later than average. Similarly, at Davis, the last flight date of *P. rapae* was unexceptional but the population densities at the end of the flight were unusually high. For both species, these circumstances translated into an unprecedented number of larvae through mid-winter.

In the Suisun Marsh, fourth- and fifth-instar larvae of *P. zelicaon* were common on Sweet Fennel, *Foeniculum vulgare* Mill. (Umbelliferae) on levees; collections were made on 28 December (4 L_5, 1 L_4, 1 L_3) and 16 January (2 L_5). In addition, one L_3 was found on the same plant at Gates Canyon in the Vaca Hills, Inner Coast Range, near Vacaville, Solano County, 1 January.

In the Davis area, a total of 67 larvae of *P. rapae* were collected from cultivated and weedy Cruciferae and *Tropaeolum* between 29 December and 15 January. Although L_1–L_3 were still numerous early in the period, only larger larvae (L_4–L_5) were taken. Numbers were so high that Cruciferous vegetables were seriously damaged in many gardens at this time.

All larvae were placed in outdoor mesh cages over fresh cuttings of their hosts, and allowed to complete development under ambient conditions. The cages were less than 0.3 km from the U.C. Davis campus meteorological station. The first pupa of *P. zelicaon* was formed 13 January and the last 24 February. 50 of the 67 *rapae* larvae were parasitized by *Apanteles (Cotesia) glomeratus* (L.) (Hymenoptera: Braconidae) and failed to pupate; 5 died of unknown causes; 12 pupated between 9 January and 28 February.

Results and Discussion

Of the nine winter *zelicaon,* 1 prepupa died of unknown causes; 5 eclosed without diapause; and 3 apparently entered diapause. Eclosions occurred on 21 and 24 February and 1, 5, and 12 March 1984. As can be seen from Table 1, these dates coincide with the flight of *P. zelicaon* in the field. (At Gates Canyon, Vaca Hills, one *zelicaon* was found as early as 19 February 1984, the earliest flight ever recorded in the region.) All the butterflies which emerged were female, as was one of the 3 diapausers.

Of the 12 healthy *rapae* pupae, all eclosed between 9 February and 24 March (seven males, five females). The flight began somewhat earlier afield but continued throughout this period.

The *Apanteles* wasps emerged without diapause in synchronized batches, each from its own host, between 24 January and 11 March—again, well-timed to parasitize first-instar larvae from eggs laid by first-brood *rapae* females. Diapause in this species is known to be under direct photoperiodic control (rather than mediated through the host, hormonally) in the U.S.S.R., but has not been studied in the introduced North American populations (Danilevskii, 1961).

The phenotypes of emerging adults of both butterflies were compared with long series of field-collected specimens from Suisun and Davis from 1984 and prior years, including many individuals which must have come from diapaused pupae, and with reared ex-diapause individuals. No phenotypic differences which might permit the detection of non-diapaused adults in the spring populations were recognized. This result confirms experimental results which indicated that the post-diapause adult phenotype is not physiologically coupled to the prior developmental arrest, but is rather a function of ambient conditions after reactivation (Shapiro, 1975a, 1978), superimposed on irreversible short-day prediapause determination.

As is evident from Table 2, low-temperature lethality is a rare event in this part of California. Although diapause may confer a degree of frost-tolerance, its principal benefit in *P. zelicaon* and *P. rapae* in north-central lowland California seems to be to delay the onset of adult development until the bulk of the rainy season has passed; thus, adult eclosion coincides with sunny, warm weather suitable for flight and hence for reproduction. Pupae accumulate enough chilling by roughly mid-January to come out of diapause; subsequent development is timed by the weather, which thus determines not only the date of first flight but the degree of synchronization of the spring brood (Shapiro, unpublished data). The unusual 1983–84 winter larvae pupated at about the same time as normal diapausing pupae would have resumed development; hence it is not surprising that their subsequent development was synchronized with the wild population. (On the other hand, diapaused pupae of *Pieris napi* L. ssp. will develop to the pharate adult at a constant temperature of 3° C, while non-diapause ones will not; hence in that species, diapausers might be expected to eclose first; Shapiro, unpublished.)

The 3 diapausing *zelicaon* presumably cannot accumulate enough chilling to break diapause in spring 1984 and will thus lay over until early 1985. This would expose them to additional risks of mortality, and in terms of contribution to the rate of population increase, place them at a great selective disadvantage relative to nondiapausing members of their 1983–84 cohort (a delay of 4 generations). Multiple-year diapause occurs in most populations of *P. zelicaon* even under normal circumstances, although it is rare in the multivoltine populations; it is especially common in univoltine foothill races which face unusually unpredictable and stressful climates and which would be expected to engage in "risk-spreading" (Sims, 1980). On the other hand, although pupae of *P. rapae* will remain viable for two years under constant refrigeration, no multiple-year diapause has ever been observed in that species under field conditions, and there is no indication that it has any physiological ability to diapause in summer (Shapiro 1975b, 1980b). Thus any diapause pupae produced by winter larvae of this species would presumably be doomed.

In a Mediterranean climate, then, a Type III diapause-induction curve permits stragglers at the end of the season to complete development and enter the reproductive pool the following spring at

Table 2. Climatic parameters for Sacramento (from U.S. Weather Bureau, NOAA Technical Memorandum NWS-WR-65, 1971). Temperatures are in degrees Fahrenheit. This table covers the period from the beginning of the last autumn generations of *P. rapae* and *P. zelicaon* to the end of the diapause in spring.

			Temperature (To 1971)				
Date	Sunrise (PST)	Sunset (PST)	daily mean	mean max	mean min	record high	record low[1]
Sept. 15	0547	1815	72	87	56	104	47
Oct. 1	0602	1749	69	83	54	98	43
Oct. 15	0615	1728	64	77	51	94	38
Nov. 1	0632	1706	59	70	47	86	34
Nov. 15	0648	1653	55	66	43	80	29
Dec. 1	0705	1645	50	59	40	71	32
Dec. 15	0716	1646	47	55	39	72	26
Jan. 1	0724	1656	46	53	39	65	24
Jan. 15	0722	1709	46	54	38	67	19
Feb. 1	0712	1728	48	57	39	68	28

Notes: [1]Low lethal temperature for *P. rapae* pupae not in diapause is ca. 22° F; for *P. zelicaon* ca. 19° F. Not determined for larvae, but both species can cool at least to the mid-20s overnight in protected micro-sites.

no disadvantage; it is a valuable hedge against off-season reproduction. In such benign climates the photoperiodic threshold for diapause inhibition may be under intermittent selection at both ends of the curve. Non-diapause overwintering may be fairly frequent in some California butterflies, especially *P. rapae.* At the latitude of Sacramento it is definitely rare in *P. zelicaon,* since midwinter larvae were not observed in the first 12 yr of this study. In coastal southern California, however, this species flies more or less all winter (Emmel and Emmel, 1973; Orsak, 1977; Shapiro, unpublished) and larvae may often be found during the shortest days of the year. Although diapause intensity is reduced and thresholds are moderately shifted relative to further north, even the San Diego populations retain the ability to diapause (Sims, 1980). How often they use it under field conditions may depend on the timing of autumn reproduction on a year-by-year basis. The hypothesis that both thresholds of a Type III curve are adaptive and under selection is testable in principle by examining latitudinal shifts in critical photoperiods.

We have had under study a culture of *P. rapae* from Xochimilco, D.F., Mexico, the southernmost (ca. 19° N) population of this species in the Americas; it also displays a Type III curve with the short-day inhibition threshold shifted upward (Shapiro, in preparation).

In climates where the onset of cold is more rapid than the change in photoperiod, that is, where strong air-mass contrasts exist and thermal lethality can occur with great suddenness, it is difficult to envision the low end of a Type III curve as adaptive. Cold nights should assure conservatism in the critical photoperiod, so that nearly all individuals will be determined as diapausers before the inhibition threshold can be reached. Larvae of *P. rapae* can be found into December and rarely into January at Philadelphia and New York City as well when early winter conditions are mild, but they never seem to survive. On the other hand, the occasional very early onset of lethal cold in such areas should select for more conservative diapause induction than the average conditions seem to warrant.

The natural selection of diapause characteristics, already complicated by its nature as a recurrent (cyclical) process operating every 4th and 5th generation, is further complicated by the ability of stochastic variation to override it occasionally in benign climates.

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BEHAVIOR OF THE ANT, *PROCRYPTOCERUS SCABRIUSCULUS* (HYMENOPTERA: FORMICIDAE), WITH COMPARISONS TO OTHER CEPHALOTINES

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INTRODUCTION

Cephalotini is a well-defined tribe of Neotropical, arboreal ants of exceptional appearance, containing about 110 species in 4 genera (Kempf, 1973). Cephalotines can be distinguished from all other ants on the basis of the proventricular valves, which are sclerotized and shaped somewhat like the head of a mushroom (Emery, 1888; Kempf, 1951). The unusually thick exoskeleton bears generous sculpturing that can include numerous striations, ridges, and flanges, as well as protective spines. The four genera have an unusually complete array of worker caste systems for such a small tribe. The genus *Procryptocerus,* containing 28 species, is typically monomorphic. *Eucryptocerus* also has a monomorphic worker caste, but contains only 3 rare species. In *Cephalotes,* workers typically have a wide size range, and in *Zacryptocerus,* worker castes range from polymorphic to dimorphic and include the most highly modified soldier forms (Kempf, 1951, 1973).

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The behavior of *Cephalotes atratus* (Corn, 1980) and *Zacryptocerus varians* (Wilson, 1976; Cole, 1980) have been examined in detail. Both Wilson (1976) and Corn (1980) stressed the importance of studying the divergent genus *Procryptocerus* in order to factor out behaviors that are related to ecological peculiarities from those tied to the evolution of polymorphism within the tribe. Among cephalotines, *Procryptocerus* appears, at least superficially, most similar to typical myrmicine ants because the head and thorax lack elaborate spines and flanges. Further, since the worker caste is monomorphic, and therefore less complex than in other cephalotines, it has been assumed to be the most primitive genus of the tribe.

The species *P. scabriusculus* is found from Mexico to Venezuela (Kempf, 1972). It nests in dead wood, principally twigs, and forms polydomous, polygynous colonies. Here I present the results of a behavioral study on workers and queens of *P. scabriusculus* as a contribution towards understanding the biology of this species and the relationship between behavior and polymorphism within the Cephalotini.

METHODS

Nests of *P. scabriusculus* were collected in Escazu, near San Jose, Costa Rica. Three clusters of inhabited twigs were taken in late August, 1983, from *Spondias purpurea*. The colony observed in this study was extracted from 3 closely spaced dead twigs and presumed to be a major part of a single colony. It contained 6 queens, 62 workers, 10 worker pupae, 1 male pupa, 49 larvae, and 27 eggs. Both trophic and normal eggs were present. One additional colony was collected in a fig tree in November, 1982.

The observation nest was a 100 × 15 mm plastic petri dish. A small test tube, containing water held back by a cotton plug, was placed in the center of the dish to provide moisture and a nest site. The petri dish fit easily on the stage of a dissecting microscope. Observations used for the ethogram were made over a period of 7 days. During this period, the colony was supplied with diluted honey and dead insects. The honey was quickly consumed by workers, but the insects were rarely touched. Occasionally, workers appeared to be drinking the body fluids of freshly killed insects. The colony was observed for a total of 20 hours, in 40 30-minute observation periods. During each 30 minute period, the nest was scanned

every 2 minutes. Therefore, if an act lasted 30 minutes, it would be recorded 15 times.

Most of the periods of observation fell between 0900 and 2300, but ants were also watched at 0200, 0400, and 0600. The colony was exposed to light from dawn (0500) until room lights were turned off (2100–0200). Under these conditions, the colony was arrhythmic; no regular differences in activity levels or types of behaviors were noted. Pupal to adult molts took place at different times of day and night. Molting is strictly tied to the biological clock in many insects, and the fact the molting was irregular suggests that the colony was physiologically, as well as behaviorally, arrhythmic.

The behavioral repertoire was analyzed using a FORTRAN program written by R. Fagen for catalogue analysis using a log normal fitting procedure developed by Bulmer (1974) (Fagen and Goldman, 1977; Fagen, 1978).

Colonies of *Zacryptocerus minutus* and *Z. christopherseni* were collected in central Panama. Various observations are reported here for comparison with the biology of *P. scabriusculus.*

RESULTS

CHARACTERIZATION OF THE FEMALE CASTES

Two characteristics of the genus *Procryptocerus* are that the worker caste is monomorphic and that queens are slightly larger but very similar to workers (Kempf, 1951). The 2 female castes are compared graphically in Figure 1, in which head width is plotted against thoracic width. The size range of workers is so narrow that this caste can be considered monomorphic. Head widths of *P. scabriusculus* workers ranged from 1.14–1.36 mm, a difference of only 0.22 mm. This is trivial in comparison to *Z. minutus* (0.96–1.7 mm) and *Z. christopherseni* (1.42–2.66 mm), 2 species with distinct soldiers. In *C. atratus* workers, head width across the occipital spines ranged from about 2–4.5 mm (Corn, 1980).

Queens are morphologically similar to workers, but can be distinguished from workers on the basis of a variety of quantitative as well as discrete differences. As shown in Fig. 1, queens can be distinguished from workers on the basis of thoracic width. Other characters that are caste-specific are abdomen width and length, thoracic morphology, including wing scars, and the presence of ocelli.

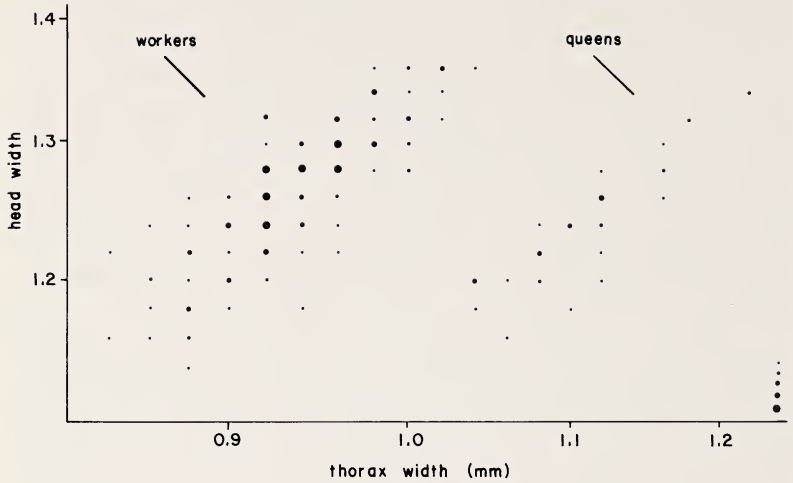

Fig. 1. Bivariate plot of morphological measurements for workers and queens. Size of filled circles indicates, in order of increasing size, 1, 2, 3, 4, and 5 or more individuals. Workers: n=136, slope=0.74, correlation=0.82. Queens: n=33, slope= 0.77, correlation=0.89. Data are from two colonies.

WORKERS

A total of 6823 behavioral acts were performed by workers and recorded over a period of 20 hours. These are presented by category in Table 1. Workers performed 31 types of acts, and, using the methods of Fagen and Goldman (1977), and Bulmer (1974), a true repertoire size of 31 was estimated. The range of the 95% confidence interval was less than 1 act. It must be emphasized that this level of accuracy applies only to the context in which the ants were observed. Undoubtedly, other behaviors would be expressed under other conditions, such as attack. Also, behaviors that are very rare or that are partially suppressed under laboratory conditions may not be recorded. Egg laying, for example, was not observed during this study. The following worker behaviors listed in Table 1 are treated in greater detail below: abdominal trophallaxis, transfer of liquid food (=regurgitation, oral trophallaxis), self-grooming, fate of infrabuccal pellets, excavating, and antennal tipping. In addition, several behaviors not included in the ethogram are discussed: stridulation, defense, and miscellaneous leg movements.

Abdominal trophallaxis

Both Wilson (1976) and Cole (1980) found that *Z. varians* exhibited a behavior rarely found in ants, abdominal trophallaxis. This behavior has not been observed in the only other cephalotine previously studied, *C. atratus* (Corn, 1980). Here I report that *P. scabriusculus* also exhibits abdominal trophallaxis. The behavior was observed primarily in individuals that had just emerged. Within hours after a worker eclosed and was able to walk, it initiated abdominal trophallaxis, licking the abdominal tip of a nestmate. Single contacts lasted as long as 30 minutes, and the same individual engaged in additional, shorter contacts over a period of several hours. Brief periods of abdominal trophallaxis between older workers and between a worker and a queen was also observed. These contacts were much shorter than the contacts involving callows, generally less than 10 seconds and frequently only 1–2 seconds.

The function of this unusual ant behavior remains unknown. The fact that callows, newly molted individuals, seek out the substance is reminiscent of proctodeal feeding so well documented in lower termites (Cleveland, 1926). Such behavior would be appropriate for transferring essential gut flora to newly ecdysed adults. Finally, it is a suspicious coincidence that cephalotines have two unusual characters apparently associated with the digestive tract: the mushroom-shaped, sclerotized proventricular valves and abdominal trophallaxis. Perhaps these ants have undiscovered dietary peculiarities.

Outside the cephalotines, abdominal trophallaxis has been reported between the slavemaking ant, *Harpagoxenus americanus*, and its host species, *Leptothorax ambiguus* and *L. longispinosus*. Workers and queens of *H. americanus* occasionally assume a stereotyped posture, with the abdomen raised, and exude a droplet of fluid which is consumed by workers of the host species (Stuart, 1981). This unusual case of interspecific trophallaxis undoubtedly has an entirely different function than the type of abdominal trophallaxis described in cephalotines which occurs primarily between callow and fully pigmented workers.

Transfer of liquid food

Workers of *P. scabriusculus* exchange liquid food at moderately high rate in comparison other cephalotines. 15.9% of total acts performed by workers involved exchange (donating plus soliciting) of

Table 1. Behavioral repertoire of *Procryptocerus scabriusculus*. Number of acts and relative frequencies observed in 20 hours.

Acts	Workers	Queens
Self-groom		
antennae and legs	1945(.2851)	75(.2517)
abdomen and legs	86(.0126)	2(.0070)
lick abdominal tip	16(.0023)	
Antennal tipping	48(.0070)	
Abdominal trophallaxis		
callow licks worker	65(.0095)	
worker licks worker	26(.0038)	
worker licks queen	7(.0010)	
Solicit and or donate liquid food		
with worker	988(.1448)	99(.3322)
with queen	99(.0145)	16(.0537)
Solicit from larvae		93(.3110)
Infrabuccal pellets		
extrude	3(.0004)	
help nestmate extrude	3(.0004)	
carry	9(.0013)	
Allogroom		
worker	1036(.1518)	4(.0134)
queen	257(.0377)	1(.0034)
Eat		
egg	75(.0110)	6(.0201)
larva or pupa	97(.0142)	
unidentified brood	13(.0019)	
honey	23(.0034)	
Lick		
egg	34(.0050)	
larva	308(.0451)	
pupa	206(.0302)	
lick molting pupa	44(.0064)	
new emergent	145(.0213)	
Manipulate, carry, drag		
egg	42(.0062)	
larva	68(.0100)	2(.0067)
pupa	17(.0025)	
callow	6(.0009)	
Excavate	908(.1331)	
Lick wall of nest	60(.0088)	

Table 1. (continued)

Acts	Workers	Queens
Debris		
carry, manipulate	178(.0261)	
lick	11(.0016)	
Total number of acts	6823(1.0000)	298(1.0000)

food with another adult ant. Since donating and begging are combined, the number must be halved to be compared to the "regurgitation with" category reported in other behavioral repertoires. This figure (8.0%) is higher than in *C. atratus,* where donating made up about less than 2% of worker acts (Corn, 1980). It is much lower than the relative frequency of exchange found in *Z. varians* by both Wilson (1976) and Cole (1980), 22.8% and 21.3% respectively, as the rate of regurgitation in minor workers. *Z. varians* soldiers have a more limited repertoire than minor workers and devote over 40% of their behavioral acts to exchange of liquid food (Wilson, 1976; Cole, 1980).

The relative frequency of exchanging liquid food in *P. scabriusculus* is moderately high in comparison to other myrmicine ants. *Pogonomyrmex badius* lacks the behavior entirely (Wilson and Fagen, 1974). In *Orectognathus versicolor,* an advanced dacetine, relative frequency of oral trophallaxis is low, between 1 and 2%, in all worker size classes (Carlin, 1981). *Leptothorax curvispinosis* (5–10%) and *L. duloticus* (4–6%) (Wilson and Fagen, 1974; Wilson, 1975), have relative frequencies similar to *P. scabriusculus.*

Self grooming

A notable feature of self-grooming in *P. scabriusculus,* compared to that of other cephalotines studied, is that abdominal self-grooming movements are performed. In workers, about 4% of all self-grooming acts involved abdominal grooming with the fore- or hind legs. The abdomen was tucked under somewhat to facilitate complete coverage. In addition, in about 1% of self-grooming acts, the abdomen was bent forward between the legs and the tip licked. Self-grooming of the abdomen has never been observed in either *C. atratus* or *Z. varians* (Wilson, 1976; Cole, 1980; Corn, 1980). The

fact that *P. scabriusculus* was able to perform this maneuver demonstrates that the loss of abdominal grooming in other cephalotines was not related to the inflexibility conferred by heavy armor. Of greater significance, the ability to autogroom the abdomen, especially the tip, casts doubt on a suggestion made by Wilson (1976) and echoed by Cole (1980) that the acquisition of abdominal trophallaxis by cephalotines was tied to loss of maneuverability.

Fate of infrabuccal pellets

P. scabriusculus workers regurgitated infrabuccal pellets and the action frequently attracted the interest of a nestmate. However, ants never ate the pellets or offered them to larvae, as has been observed in *Z. varians* (Wilson, 1976; Cole, 1980). As soon as a pellet was regurgitated, a worker would leave the brood area and drop the pellet onto the floor of the petri dish. Regurgitation of infrabuccal pellets was never observed in *C. atratus* (Corn, 1976).

Excavation

Usually several workers were at the rear of the nest tube digging at the damp cotton with their legs and mandibles. Presumably this behavior would be homologous to excavating the blind end of a tunnel in a twig nest.

Antennal tipping

A stretching behavior dubbed antennal tipping by Wilson and Fagen (1974) was frequently observed. This behavior has been noted in many ant species, including *Leptothorax curvispinosis, L. duloticus* (Wilson, 1975), *Formica perpilosa* (Brandao, 1978), *Colobopsis* sp. (Cole, 1980), *C. atratus* (Corn, 1980) and *Z. varians* (Wilson, 1976; Cole, 1980). In *P. scabriusculus,* the first pair of legs were extended forward and the rear 2 pairs extended backwards. The body was elevated due to the leg extension and the abdomen drooped slightly. The position of the head was more variable. Sometimes it was raised and sometimes it was tucked under the body. The impression was one of rigidity, and the body sometimes trembled slightly or the antennae vibrated.

Stridulation

Both workers and queens stridulated when physically trapped or restrained. This behavior does not appear in the behavioral reper-

toire (Table 1) since it was produced only when ants were held and not under the standard conditions for observation. When an ant was provoked into stridulating, nearby nestmates did not obviously alter their behavior. The stridulatory file is located on the neck of the gaster where it inserts into the post-petiole.

The presence and use of a stridulatory organ in *Procryptocerus* is remarkable as it is found in no other genus of cephalotines. The absence of a stridulatory organ in the Myrmicinae is unusual; Markl (1973), in a survey of stridulatory structures in ants, found that 83% of myrmicine genera had them. So, it is intriguing first, that most cephalotines have lost the file and second, that *Procryptocerus* has retained the structure. Markl (1973) found the stridulatory organ in all 7 species of *Procryptocerus* he examined.

Four subfamilies of ants have stridulatory organs: the Nothomyrmeciinae, the Pseudomyrmicinae, the Ponerinae and the Myrmicinae (Sharp, 1893; Haskins and Enzmann, 1938; Markl, 1973; Taylor, 1978). The stidulatory organ is always found on the same pair of segments: the file is located on abdominal segment IV and the scraper on segment III. In view of the apparent evolutionary stability of the stridulatory organ's position, its presence in *Procryptocerus* can be regarded as a reliable primitive character.

The ability to stridulate is common in ants, but the role of stridulation in communication has been demonstrated in only two cases. Markl (1965) showed that stridulation serves as a distress signal in *Atta cephalotes*. Buried workers stridulate and nestmates respond by digging in the vicinity of the sound. Markl and Hölldobler (1978) have shown that in *Novomessor,* stridulatory signals function as a mechanism for modulating responses to other stimuli. For example, food retrieving behavior was enhanced when chemical recruitment stimuli were received concurrently with stridulatory signals. *Novomessor* stridulates spontaneously, without the provocation of physical restraint.

Neither of these proven roles of stridulation applies directly to *P. scabriusculus*. Digging is not an appropriate rescue response in an arboreal nest, and the fact that *P. scabriusculus* does not stridulate spontaneously, without restraint, argues against an analogy with *Novomessor*. A third possibility is that stridulatory vibrations deter predators. This phenomenon has been documented in insects other than ants (see Masters, 1979).

Defense

P. scabriusculus relies almost exclusively on its thick exoskeleton, with cephalic scrobes to shield the antennae, to discourage enemies and predators. In response to real or supposed threats (other ants, freshly killed flies, seeds, flowers, pollen, etc.), workers lowered their heads, contacted the object, and pushed. The workers also nipped as best they could with their small, blunt mandibles. *P. scabriusculus* was ineffective in coping with enemy ants in the open. One colony in a petri dish took 12 hours to clip the legs off a *Pseudomyrmex* sp. worker placed in the nest. Presumably bulldozing would be more effective inside a twig nest in preventing trespassers from entering and nipping would be more effective where the enemy could be pinned against the walls of the narrow passageways.

Leg movements

Another behavior not included in the repertoire is miscellaneous leg movement. When ants were inactive, standing quietly in position, often 1, 2, or, rarely, 3 of their legs might be moving. Most of the movement was made by the tibia and tarsus, which were swung as a unit, while the femur stayed in place. Often, the femur was flexed and also participated in the movement. About 60% of the time the movement involved one of the rear legs, 30% a middle leg, and 10% a front leg. The behavior was observed in queens as well as workers.

QUEENS

Number of queens

P. scabriusculus has multiple queens. The colony observed in this study contained, at the time of collection, 6 dealate queens and 62 workers (8.8% queens). After the study was terminated, the colony was preserved in alcohol. Subsequent dissection showed that all 6 queens had fully developed ovaries. In addition, 3 queens (#1, #4, and #6) contained at least one egg large enough to fall in the size range of viable eggs. Two fragments of other colonies contained 4 queens with 40 workers (9.1%) and 1 queen with 17 workers (5.5%). A large colony collected in November, 1982, contained 72 workers with 27 queens (27%). In this colony, many of the queens had unexpanded, crumpled wings indicating that they had been produced within the colony and were not primary, founding queens.

In ants, polygyny evolves under special ecological conditions, such as short-lived nest sites (Hölldobler and Wilson, 1977). Therefore, it is not a reliable indicator of major phylogenetic trends within a group. Apparent polygyny (the presence of multiple dealate queens) is scattered throughout the advanced genus *Zacryptocerus*. In *Z. texanus*, Creighton and Gregg (1954) (see also Creighton, 1963; Creighton, 1967) found colonies and colony fragments containing 0–14.7% queens. In *Z. christopherseni*, I found 13 dealate queens in a single colony containing over 4,000 workers and soldiers. In contrast, *Z. rowheri* (Creighton and Nutting, 1965), *Z. pusillus* (Limongi, 1977), *Z. varians* (Wilson, 1976), *Z. minutus* (personal observation), as well as *Cephalotes atratus* (Corn, 1980) and *Eucryptocerus placidus* (Corn, 1976) are apparently monogynous.

Behavior of queens

Queens performed a total of 298 acts in 9 categories over a period of 20 hours (Table 1). When data were fitted to a lognormal Poisson distribution (Fagen and Goldman, 1977), the true repertoire size of queens in a laboratory nest was estimated to be 11, with a 95% confidence interval of ±3, types of acts.

The entire repertoire of queens, with the exception of self-grooming, was devoted to eating. Queens solicited and received food not only from workers but also from larvae. Queens used antennal soliciting movements and licked larvae vigorously around the mouth to demand food. This behavior is similar to that described for queens of *Leptothorax curvispinosus*, which solicit labial gland secretions from larvae (Wilson, 1974).

Most of the queens' infrequent behaviors, shown in Table 1, were probably associated with behavioral sequences leading up to demanding food from workers or larvae. For example, grooming of workers preceded solicitation movements with the antennae. Manipulation of larvae, moving them into a better position, was a prelude to solicitation behavior.

P. scabriusculus queens, which performed acts in 9 behavioral categories, were more versatile than queens of *Z. varians*. In *Z. varians*, queens performed only 3 acts: self-grooming, regurgitating with minor workers, and laying eggs (Wilson, 1976; Cole, 1980). Outside the Cephalotini, 5 repertoires of queens are available. Repertoire size ranges from 5 in *Colobopsis* sp. (Cole, 1980) and

Leptothorax curvispinosus (Wilson and Fagen, 1974) to 8 in *Orectognathus versicolor* (Carlin, 1981), 9 in the slavemaking species, *Leptothorax duloticus* (Wilson and Fagen, 1974), and 16 in the primitive ponerine, *Amblyopone pallipes* (Traniello, 1982). In respect to other ant species, then, the repertoire size of *P. scabriusculus* queens appears to be average. In comparison to the queen of *Z. varians,* however, the queen of *P. scabriusculus* is much less behaviorally specialized.

Variation in behavior of individual queens

To determine if there were differences in the behavior of individual queens that might reflect reproductive dominance, queens were marked with colored paint and the acts of each recorded for 15.5 hours of the study. The most common acts in which queens participated were soliciting liquid food from workers, soliciting liquid food from larvae, self-grooming movements, and being groomed by a worker (Table 2). For comparison, the average number of similar acts recorded for workers during the same 15.5 hour period is also shown in Table 2.

The 6 queens showed considerable variation in their rates of soliciting liquid food. A chi-square test showed that pattern of queen behavior was significantly different from an even distribution for both soliciting food from workers ($p<0.025$) and soliciting food from larvae ($p<0.005$). The amount of food that queens were able to collect from workers and larvae could be directly associated with rank, the amount being an indication of resources convertible to

Table 2. Behavior of individual queens. Values given are actual numbers of acts in a category that were performed by each individual in 15.5 hours of observation. The average queen values are means of acts performed by the six queens. The value for average worker is the number of acts in a category performed by workers in 15.5 hours of observation divided by the number of workers (n=62). Queens solicited from larva by antennating and licking larvae around the mouth. Workers licked larvae as part of brood care and did not concentrate in the head region. Values of p for differences among queens were determined using a chi-squared test.

Queen #	1	2	3	4	5	6	av. queen	av. worker	p
Solicit from worker	13	16	5	23	9	11	13	7	<.025
Solicit from/lick larva	7	12	7	25	13	10	12	4	<.005
Self-groom	12	10	12	4	8	2	8	25	<.005
Groomed by worker	26	39	40	35	43	31	36	15	ns

viable eggs. In soliciting, queen #4 clearly led all the rest, while queen #3 was the clear loser. The least demanding queens participated in food exchange with workers at a rate similar to workers: such queens can be regarded as worker-like in their behavior (Table 2).

Occasionally, queens solicited from other queens (n=9). One queen would initiate the contact, but both would perform soliciting movements with their antennae. No food appeared to be exchanged during these bouts. The number of queen–queen contacts was not directly correlated with rank as determined by rates of queen–worker and queen–larvae exchanges. The sample size is so low, however, that it is premature to dismiss the possibility that rank is determined or maintained by such interactions.

The relationship between grooming patterns and rank, if one exists, is not clear (Table 2). There were significant differences among queens in the amount of self-grooming indulged in ($p<0.005$, chi-squared test), but the difference in attention received from workers was not significant. Queens groomed themselves less than the average worker and were groomed by workers more often than workers groomed each other. No queen could be classed as worker-like in grooming behavior.

Viable and trophic eggs

Both normal, viable eggs and trophic eggs are found in *P. scabriusculus* colonies. Viable eggs in *P. scabriusculus,* those capable of embryogenesis, were large and cylindrical, measuring 1.32–1.66 mm long. The shape is typical of Cephalotini, as well as other arboreal ants (Wheeler and Wheeler, 1954). Smaller, presumably trophic, eggs were highly variable in size (0.6–1.2 mm). Trophic eggs were less cylindrical than viable eggs and had a milky, homogeneous appearance. Generally, ants consume trophic eggs immediately after they are laid (Wilson, 1971). Why *P. scabriusculus* should allow non-viable eggs to lie around is a puzzle.

The relative capabilites of egg laying in workers and in queens is not known, since no egg laying was observed. In other cephalotines, workers are known to lay trophic eggs as well as viable, unfertilized eggs that develop as males. In *Z. varians,* minor workers lay trophic eggs (Wilson, 1976), and production of males by queenless colonies has been noted in *C. atratus* (Weber, 1957), *Z. varians* (Wilson, 1976) and *Z. minutus* (personal observation).

Discussion

Can a comparison of behaviors within the Cephalotini contribute to an understanding of the phylogeny within the tribe or of the evolution of morphological worker castes? Including the behavioral data reported here, information is available for the three major genera of cephalotines: *Procryptocerus, Cephalotes, and Zacryptocerus.* It is now possible to compare and integrate behavioral with morphological data in considering phylogenetic relationships among cephalotines.

Only behavioral characters that do not occur in all members of a group can be useful in constructing alternative paths of evolution. Six such characters known for three species of cephalotines are listed in Table 3. First, I will use these characters to illustrate overall behavioral similarities between species. Then, the polarity (ancestral vs. derived state) of these characters will be surmised and used to construct behavioral cladograms (Fig. 2). Finally, the evolutionary relationships suggested by the cladogram can be used to re-examine our assumptions about the evolution within the cephalotines and their diverse morphological worker castes.

P. scabriusculus has been characterized as morphologically divergent (Kempf, 1951), quite discrepant (Kempf, 1973), and primitive (Corn, 1976; Wilson, 1976). In its behavior, however, it shares a remarkable number of traits with the advanced species, *Z. varians* (Table 3). Table 3 indicates that *P. scabriusculus and Z. varians* share four of the six discrete behavioral characters listed, two of

Table 3. Comparison of behavioral characters among three cephalotine species, representing the three major genera. The six behaviors that are listed may have phylogenetic significance. An asterisk (*) indicates which behavioral state is considered derived. Note that *Procryptocerus scabriusculus* and *Zacryptocerus varians* share four characters, while *Z. varians* and *Cephalotes atratus* share two. *P. scabrius-culus* and *C. atratus* share none of the six behavioral states. Abbreviations given are used in Figure 2.

	Cephalotes	*Zacryptocerus*	*Procryptocerus*
Abdominal trophallaxis (at)	no	(yes*	yes*)
Adult transport (car)	yes	(no*	no*)
Infrabuccal pellets	no*	(yes	yes)
Lay trophic eggs	no*	(yes	yes)
Stridulate (str)	(no*	no*)	yes
Abdominal self-groom (ag)	(no*	no*)	yes

which are primitive. *Z. varians* and *C. atratus* share only two characters, while *P. scabriusculus* and *C. atratus* share none. *P. scabriusculus* and *C. atratus* are both considered relatively primitive, but behaviorally they are primitive in different ways.

On the basis of morphological characters, Brown (1973) felt that all cephalotine genera besides *Procryptocerus* could be lumped. Kempf (1973) maintained the distinction betwen the genus *Cephalotes* and *Zacryptocerus*. The behavioral data show that *C. atratus* is divergent from both *P. scabriusculus* and *Z. varians* and therefore support the generic distinctions proposed by Kempf (1973).

The probable polarity (ancestral vs. derived state) of each of the characters in Table 3 can be assessed by outgroup comparisons with other ants. The closest relatives of the Cephalotini are, unfortu-

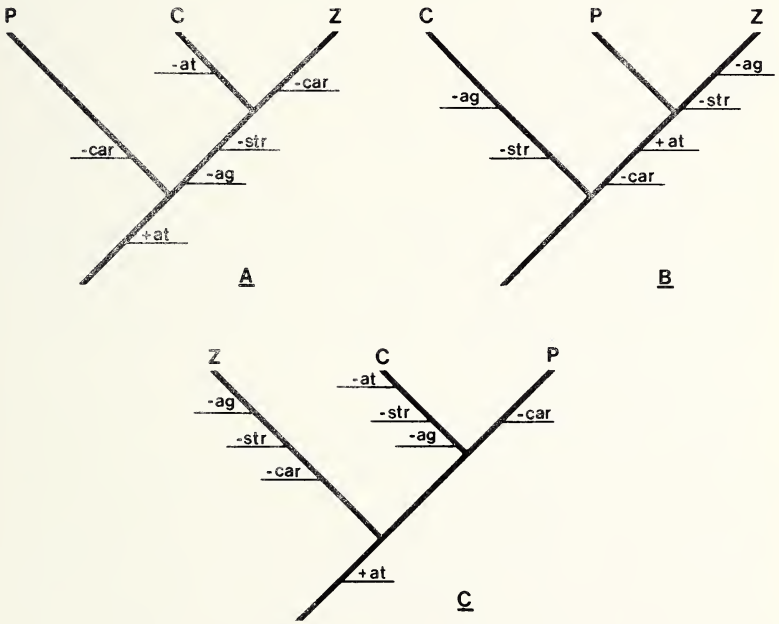

Fig. 2. Cladograms for 4 synapomorphic characters in 3 species of cephalotines: *Procryptocerus scabriusculus, Cepahlotes atratus,* and *Zacryptocerus varians.* The ancestral cephalotine is assumed to have had the following profile: −at (abdominal trophallaxis), +ag (abdominal grooming), +str (stridulation), +car (adult transport =carrying nestmate).

nately, not known. Therefore, cephalotines are compared with other myrmicines, when that information is available, as well as with other subfamilies. Two important behaviors, abdominal trophallaxis and stridulation (see Table 3), were discussed in detail above. Adult transport, in which one adult carries another, occurs widely in ants, and is especially well developed and stereotyped in the Myrmicinae and the Formicinae (Wilson, 1971; Möglich and Hölldobler, 1974). Therefore, the expression of this behavior is considered the primitive condition in the Myrmicinae and its loss the derived state.

Behavioral Cladograms

Cladograms provide a useful device for examining possible ways different sets of characters could have evolved. I will assume that the three species, *P. scabriusculus, C. atratus,* and *Z. varians,* are monophyletic, *sensu* Hennig (1966); no species is an ancestor of either of the others. I also assume that the three species involved are representative of their genera. Recognizing that this second assumption may be premature, I stress that more species need to be studied, especially in the diverse genus *Zacryptocerus.*

The most useful characters in constructing cladograms are those that are synapomorphic, derived traits that are shared. There are three ways that three species could have evolved such that two now share an advanced trait. The simplest is that the two species share a common ancestor that possessed the character. The second and third ways require two steps. First, the two species could have evolved the trait independently. Secondly, all three species could have acquired the trait from a common ancestor, and one species subsequently lost it.

There are four synapomorphic characters in Table 3. Abdominal trophallaxis and absence of adult transport are shared by *Z. varians* and *P. scabriusculus* while absence of stridulation and of abdominal self-grooming are shared by *Z. varians* and *C. atratus.* Of the three possible cladograms using these four traits (Figure 2), two appear equally plausible. In both cladogram *A* and *B*, two of the four synapomorphies require two steps to generate the appropriate distribution of characters. Two steps means independent derivation of the characters, or common derivation and secondary loss. The third cladogram, *C*, can be rejected as unlikely by parsimony since all four synapomorphies require two steps to produce the appropriate pattern.

When the relative importance of characters is considered, cladogram *A* gains plausibility over *B*. The ability to stridulate has rarely been lost in the Myrmicinae (Markl, 1973). Therefore, a single loss (cladogram *A*) can be considered more likely than a double one (cladogram *B*). Similarly, abdominal grooming movements occur in almost all ants (Wilson, 1962; Farish, 1972); loss is probably a rare evolutionary event. The appropriate pattern of abdominal grooming is derived most parsimoniously in cladogram *A*. Adult transport (carrying) on the other hand is a character expressed to widely varying degrees among the ants. Nestmate carrying, used primarily during emigration to new nest sites, may be relatively easy to lose if it becomes unnecessary ecologically. The adult transport character then does not lend strong support to either cladogram. Finally, the appropriate pattern for abdominal trophallaxis is derived most parsimoniously in cladogram *B*. In cladogram *A*, *Cephalotes* loses this character secondarily. Since intraspecific abdominal trophallaxis rarely occurs in ants, and is poorly understood, the difficulty or ease of its subsequent loss cannot be evaluated. In summary, on the basis of a character by character evaluation, cladogram *A* is more plausible.

Implications for the Evolution of Worker Polymorphism

Monomorphism is the ancestral state of the worker caste in most ants and probably represents the ancestral state of the Cephalotini as well. In myrmicines, a few cases of secondary monomorphism are known in species with workers that are minute in comparison to the queen (Wilson, 1953, 1971). If worker monomorphism is accepted as the ancestral state in the Cephalotini, then cladogram *A* provides the most parsimonious derivation of the pattern of worker polymorphism. Cladogram *B* implies that the morphological worker caste systems characteristic of *Zacryptocerus* and *Cephalotes* evolved independently. According to cladogram *A*, the tendency to express morphological diversity within the worker caste evolved once. *Cephalotes* maintained a weak bimodality in the size frequency distribution over a wide size range (Corn, 1980), while the *Zacryptocerus* line intensified that bimodality, a trend which led to the completely dimorphic worker caste of some species.

If worker monomorphism is ancestral and *Procryptocerus* represents a relict state, it follows that, in the Cephalotini, soldiers must

be the primitive caste and minor workers the novel caste. In *Procryptocerus*, workers closely resemble the queen as do soldiers in *Zacryptocerus* and large workers in *Cephalotes*. Advanced cepalotines appear to have added smaller workers to their worker caste systems. Soldiers of *Zacryptocerus* fulfill the first of two criteria proposed in Wilson (1980) for a primitive caste: they resemble the workers of the less modified, monomorphic members of the same tribe (e.g. *Procryptocerus*). *Zacryptocerus* soldiers do not meet the second criterion, that the primitive caste perform the generalized services of a colony. Wilson (in press) has discovered that *Pheidole* soldiers can be induced to express behavior typical of a minor worker's repertoire; morphological specialization does not preclude behavioral flexibility. This discovery uncouples morphological and behavioral specialization and may relax the need for a primitive caste meeting the second criterion of generalized behavior.

Ecological Similarity

Ecological similarity between species can contribute significantly to similarities in behavioral traits. Cole has demonstrated that two species of ecologically similar but phylogenetically distant species of ants, *Z. varians* (Myrmicinae) and *Colobopsis* sp. (Formicinae) exhibit convergence of qualitative behavioral traits as well as of quantitative aspects of their repertoires. Both species inhabit hollow twigs of a variety of plants that represent dry habitats (Smith, 1923; Kempf, 1958; Cole, 1982).

Z. varians and *P. scabriusculus* are also ecologically similar. Both nest in hollow, dry twigs, and the ants themselves are of similar size. In *Z. varians*, minor workers measure 3.6–4.7 mm and soldiers 5.9–6.3 mm in total length (Kempf, 1958). The size of *P. scabriusculus* workers falls between the two castes of *Z. varians*, with workers measuring 4.6–5.2 mm in total length. The colony size of both species is also small, not exceeding several hundred workers. In addition, *Z. varians* is known to be nocturnal, and *P. scabriusculus* is believed to be nocturnal of crepuscular (Snelling, 1968).

C. atratus, in contrast, is a large ant (8–14 mm total length), nesting in spacious cavities in living wood. Colony size is extremely large compared to other cephalotines, with about 12,000 workers in a mature colony. They forage diurnally. Corn (1976) suggests that many of the differences between *C. atratus* and *Z. varians* might be based on the differences in nest site. Use of infrabuccal pellets as

food and high rates of regurgitation are adaptations to dry conditions (Wilson, 1976; Cole, 1980), and would not be necessary in *C. atratus* which nests in moist tree cavities (Corn, 1976). The relatively wide nest chambers of *C. atratus* may have provided an environment in which the primitive behavior of carrying nestmates was possible, and ultimately, retained (Corn, 1976). The lack of both infrabuccal pellets and abdominal trophallaxis may be indicative of an entirely different diet in *C. atratus* than either *P. scabriusculus* or *Z. varians.*

In summary, some of the behavioral similarities between *P. scabriusculus* and *Z. varians,* and the apparent divergence of *C. atratus,* may be based in ecology rather than phylogeny. Behavioral convergence of *P. scabriusculus* and *Z. varians* would lend further support to cladogram *A*.

Summary

P. scabriusculus is a cephalotine with multiple queens and a monomorphic worker caste. Differences in the behavior among individual queens suggest that queens are not equal in reproductive status. Newly emerged *P. scabriusculus* workers indulge in prolonged periods of abdominal trophallaxis. Abdominal trophallaxis has been reported previously in *Z. varians,* an advanced cephalotine with a dimorphic worker caste. Cladograms based on behavioral characters support a phylogenetic scheme in which the divergence of *Procryptocerus* occurred prior to the divergence of *Cephalotes.* Within the Cephalotini, the minor workers, rather than soldiers, appear to be the novel worker caste.

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MALE AGGRESSION AND FEMALE EGG SIZE IN A MATE-GUARDING AMBUSH BUG: ARE THEY RELATED?*

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Introduction

The term "mate guarding" implies some form of active defense of a mate by the guarding individual. We previously described aspects of the mating system of *Phymata fasciata* (Hemiptera: Phymatidae) including the first report of mate guarding for this family (Dodson and Marshall 1984). In the present report male *P. fasciata* aggressive behavior is described and found to be in accordance with the expectations of mate guarding. In addition, we relate female size to egg size and discuss how this relationship may play a role in the evolution of guarding behavior.

Methods

Ambush bugs were observed on prairie sunflower (*Helianthus petiolaris*) in north central New Mexico. Because of low bug densities (see Dodson and Marshall 1984), encounters between single males and males guarding females were infrequent. Three naturally-occurring, guarding male:single male interactions were observed in 1982. In addition, 13 interactions were "manipulated" in the field to corroborate the accuracy of our natural observations. Manipulations involved transferring a single male to a flower already occupied by a mating pair. The transferred individual was placed as far from the pair as possible and then observed until it approached the pair or left the plant. Although there were some minor variations, three basic components of male:male interactions (see below) were the same for natural and manipulated cases. Most of the behaviors described here were also performed by bugs kept on plants in the lab.

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Assuming egg shape to approach that of a cylinder, we estimated volume of all chorionated eggs (EV) of 21 *P. fasciata* females using length and width as measured with an ocular micrometer.

Results and Discussion

When not actually copulating with a female, males rode in an amplexed position on the female dorso. Approach by a second male initiated a series of actions (Table 1). There were three components to these male interactions: orientation by the guarding male towards the intruder; stridulation by the guarding male; and an aggressive or nonaggressive action associated with contact by the intruder. Guarding males oriented towards intruders by rotating their whole body atop the female. Stridulation, audible to us at close range, involved scraping the beak back and forth across a file on the sternum. Often the guarding male began stridulating immediately upon approach by the intruder and occasionally continued even after the intruder's departure.

Contact by the intruder resulted in one of three behaviors by guarding males. Guarding males were either 1) passive (i.e., held their same position on the female whatever the intruder did) 2) repositioned themselves so as to have their bodies always between the female and the intruding male, or 3) physically attacked the intruder. Attacks involved the use of the raptorial fore legs and were sometimes quite vigorous. We saw males grasp an intruder's antenna for long periods and in one natural occurrence a guarder literally lifted his opponent off the substrate. No injuries were known to have resulted from this aggression, but individuals were seen with excised antennae and tarsae.

Only one displacement of a guarding male was seen in the field and it was short-lived. After being maneuvered out of the amplexed position by an intruder, the original male immediately climbed on top of the pair and began shaking vigorously back and forth. This action eventually resulted in both males toppling to the ground, and then moving further from the female's position. On two occasions in the laboratory similar separations of interactant males from females were observed. These apparently resulted from intruder males rocking vigorously while on top of paired males.

In summary, mate guarding in *P. fasciata* is active and can be highly aggressive. It is also time-intensive. Typically, pairs already

Table 1. Frequency of behaviors of guarding males observed in 16 interactions involving intrusions (natural and manipulated) of unpaired males in the field on *Helianthus petiolaris*.

			Response of guarding male upon contact by intruder				
	Orientation toward intruder	Stridulation upon intruder arrival	Agressive attack	Blocking maneuver (repositioning)	Passive Maintenance of original position	Departure by intruder	Stridulation after intruder departure
Present	12	10	8	5	3	15	3
Absent	4	0	8	11	13	1*	4
Undetermined	0	6	0	0	0	0	9

*Both males were separated from female (see text)

in amplexus upon our arrival in the field were still together several hours later when we departed. Pairs on flowers in the laboratory stayed together overnight. We found that these males were guarding females both prior to and following copulation (Dodson and Marshall 1984).

Presumably time spent with one female, particularly after copulation has taken place, decreases a male's opportunities for copulations with additional females. Why, then, might males be employing this guarding tactic? One possible answer is that the low population densities favor males that, upon finding a female, remain with her and actively repel other males. If such an attempt to monopolize a potential mate increased the chance of successfully copulating with her, precopulatory guarding might be a better tactic than spending this time searching for other females. This, however, seems an unlikely explanation for postcopulatory mate guarding. Parker (1970) argued persuasively that postcopulatory defense of a mate (preventing other males access to her) is an evolved strategy to counter sperm competition from potential, subsequent male mates. Although nothing is known regarding sperm precedence in ambush bugs specifically, most evidence for insects shows an insemination advantage for the last male to mate (Walker 1980).

We feel there is another factor that may be important to our understanding of mate guarding in these ambush bugs (and perhaps in other insects). This factor is male preference for particular females. At one of our study sites, males were paired with females that were heavier than females without males (Dodson and Marshall 1984). These paired females also had more eggs than single females. The apparently superior fecundity of these females seemed to us to be a potential fitness gain for males. To further investigate the possible adaptiveness of selective pairing by males we looked at egg size within females. We had previously determined the wet weight (WW), pronotal width (PW) and femur length (FL) of these same females. All 3 measurements were significantly correlated with egg volume (BW: $r = .60$, $p = .003$; PW: $r = .61$, $p = .003$; FL: $r = .62$, $p = .002$). The 3 measurements are so highly correlated with each other, the residual variation examined by partial correlations was found to be negligible ($r_{EV\ FL \cdot WW\ PW} = .04$, $p = .84$; $r_{EV\ PW \cdot WW\ FL} = .24$, $p = .31$; $r_{EV\ WW \cdot PW\ FL} = .27$, $p = .25$). Therefore, all 3 variables are approximately equivalent predictors of egg volume. We believe,

as Johnson (1982) suggested, that this could potentially provide males with a basis for discriminating the most reproductively fit females. Males capable of assessing a cue to female fitness could "decide" whether to remain with a particular female or search for another. This would explain our findings of large females most often in pairs. Such a tactic could be even more feasible in insect populations which occur in high densities. The resulting high encounter rates would mean less time spent searching for more suitable mates.

This hypothesis assumes that larger eggs enhance the success of resultant offspring (e.g., through increased nutrient provisions or greater competitive ability of larvae). Such advantages are controversial, but the rather limited data do yield some support. Relationships between egg size and offspring success in insects have been addressed by Capinera (1979 and references therein), Richards and Myers (1980) and Barbosa, et al. (1981).

Discrimination of mates by males has been shown in several species in which males are contributing relatively large amounts of paternal care or other benefits (for insect examples see Thornhill and Alcock 1983). Perhaps more significant for this discussion are the findings of mate discrimination by males of noninvesting species (Loiselle; 1982; Verrel 1982; Hatziolos, M. E. and R. L. Caldwell 1983; references in Thornhill and Alcock 1983; Johnson and Hubbell, unpublished). Although some of the latter examples are laboratory experiments, the fact that the apparently adaptive behavior is exhibited suggests that selection under natural circumstances must be occurring at significant levels.

Several recent papers have reported overrepresentations of larger females within mating populations of insects. Such biases, based on either size or weight, have been found in beetles (McCauley and Wade 1978, Johnson 1982 and McLain 1982), pierid butterflies (Marshall 1982), ambush bugs (Dodson and Marshall 1984) and tephritid flies (Dodson, submitted). It would be interesting to determine the relationship between female body size and egg size in all such species in light of a male mate discrimination hypothesis.

McCauley and Wade (1978) showed that mating male and female soldier beetles, *Chaulignathus pennsylvanicus,* were heavier than nonmating males and females based on dry weights. They considered dry weight to be an index of body size and suggested larger

females could be preferentially mating with larger (and presumably more fit) males by physically resisting mating attempts by all males and escaping the smaller ones. They further postulated that larger females might be "somewhat more receptive than small females". However, except for the suggestion that receptivity might be related to egg development, they did not account for the paucity of small females in the mating population. Woodhead (1981) offered what appeared to be a more parsimonious explanation. She found that mating females had larger eggs than "rejecting" females and proposed that heavier female soldier beetles were more often found mating because they were more reproductively mature and therefore more receptive to mating. Woodhead (1981) did not discuss her choice of eggs for measurement. She did state that soldier beetles "mature eggs in groups" and so we assume that all primary oocytes were measured, including many not yet fully-yolked. Even if this were the case, however, her measurements are also consistent with the hypothesis that females differ in ultimate egg size and not just developmental stage.

In many insects, oocytes are in various stages of development within the ovaries throughout most of a female's adult life. This makes comparative measures of all eggs virtually impossible because of the miniscule size of the youngest oocytes. For valid comparisons between females, age classes of eggs must be delineated. Typically, fully-yolked eggs are chosen because they are easily defined, relatively easy to distinguish (although not always), and supposedly will not get any larger. We avoided this problem by measuring only chorionated eggs, i.e., eggs that are fully grown with their "shells" encasing them. Thus, we have demonstrated variation in egg sizes between females which are independent of sexual maturity and apparently dependent on female size.

In summary, we have shown that *P. fasciata* males, when paired with females, aggressively fend off intruding males and that larger females produce larger eggs. Previous work (Dodson and Marshall 1984) revealed that males were more often paired with larger rather than small females in a natural population. All of these factors are consistent with the hypothesis that given some choice, males will preferentially guard mates which provide a higher reproductive potential.

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ON THE METAPLEURAL GLAND OF ANTS

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Introduction

The metapleural gland (also called metasternal or metathoracic gland), a complex glandular structure located at the posterolateral corners of he alitrunk is peculiar to the ants. Although the gland was noted by Meinert (1860) and Lubbock (1877), it was Janet (1898) who conducted the first detailed anatomical study of this organ, as part of his classic work on *Myrmica rubra.* Additional details have been added by Tulloch (1936) on *Myrmica laevinodis;* by Whelden (1957a, b, 1960, 1963) on *Amblyopone* (*Stigmatomma*) *pallipes, Rhytidoponera convexa, R. metallica, Eciton burchelli, E. hamatum;* by Tulloch et al (1962) on *Myrmecia nigrocincta;* and by Kürschner* (1970) on *Formica pratensis.*

It is generally assumed that the metapleural gland is a universal and phylogenetically old character of the Formicidae. Even the extinct species *Sphecomyrma freyi* of Cretaceous age appears to have possessed a metapleural gland (Wilson et al 1967a, b) and the organ is well developed in the most primitive living ant species *Nothomyrmecia macrops* (Taylor 1978) (see Fig. 2).

In the course of our current comparative study of the internal and external anatomy of exocrine glands in ants, we discovered that the metapleural gland is absent or significantly reduced in several ant genera where such reduction had not been previously suspected. In addition we observed a widespread absence of the metapleural gland in males among ant species.

Our survey is far from complete, even at the generic and tribal levels. We think, however, that the pattern revealed by our observations is important enough to warrant a short publication at this time.

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*Kürschner apparently was not aware that the paired thorax gland near the petiole she described was the metapleural gland.

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Results

The metapleural gland is a paired structure. Each side consists of a cluster of glandular cells, and each cell is drained via a duct into a membranous collecting sac that Tulloch et al. (1962) called secretory recess. The collecting sac leads directly into the storage chamber or atrium (receptacle, sensu Tulloch et al. 1962), a sclerotized cavity. Externally the metapleural gland is often marked by a pronounced vault (bulla), and a slit-shaped opening to the outside (Fig. 1).

Although the metapleural gland is present in most ant species, it nevertheless varies greatly among them in size and shape (Figs. 2 & 3). Table 1 lists all of the ant species for which we obtained complete series of longitudinal sections through the mesosoma. The specimens were fixed in alcoholic Bouin or Carnoy, embedded in methylmethacrylate and sectioned 6 to 8μ thick. The staining was Azan (Heidenhain). We attempted to obtain approximations of the number of glandular cells either by counting the cells with clearly visible nuclei or by counting the number of duct openings in successive sections.

The data reveal a considerable variation in the size of the metapleural gland among different species. Even more significantly, our study established that the gland is absent in *Oecophylla longinoda* and *O. smaragdina* (Fig. 4), in all species of *Camponotus* and *Polyrhachis* sectioned, and in *Dendromyrmex chartifex* (Tab. 1).

We extended this list by an additional survey of the external features that indicate the presence of the metapleural gland, using light-stero-, and scanning electrone microscopy. Of 27 species of *Camponotus* investigated, only *C. gigas* showed a slit-shaped opening in the posterior metapleural region (Fig. 5c). In all other *Camponotus* species the metapleural gland is clearly absent (Fig. 5a, b; Tab. 2). This confirms the suggestion of Ayre and Blum (1971) based on external inspection of *Camponotus pennsylvanicus* workers that this species might not possess a metapleural gland. In none of the species of *Polyrhachis* investigated did we detect any signs of a metapleural gland (Tab. 2). In addition our study revealed that in several species whose workers and queens have well-developed metapleural glands, the males do not possess this organ; whereas in other species the males have large metapleural glands (Tab. 1).

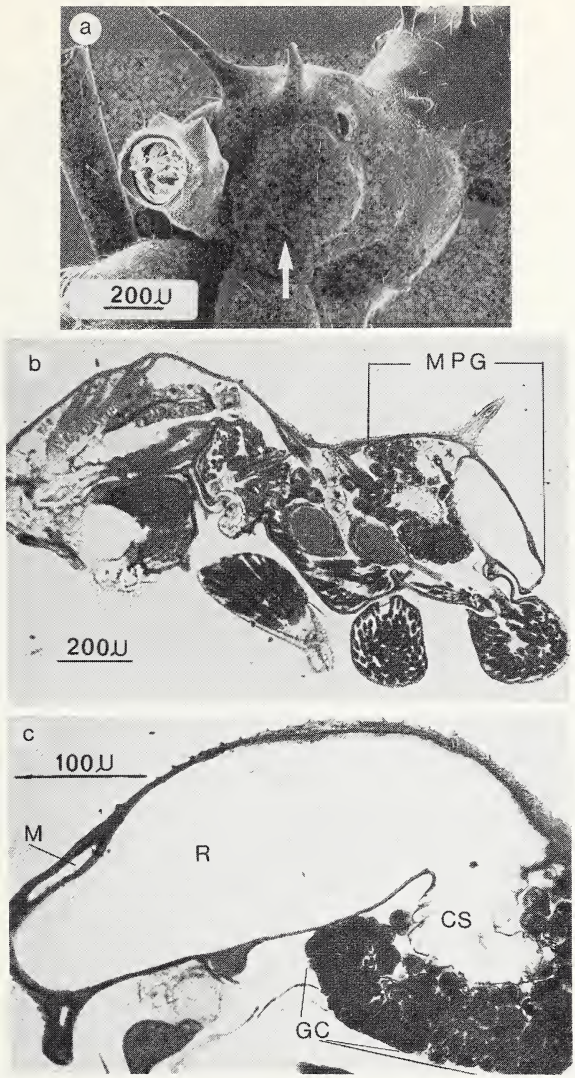


Fig. 1. The metapleural gland of *Atta,* illustrating the major anatomical feature of this organ. a. SEM micrograph of the mesosoma of *A. cephalotes,* showing the large pronounced vault (bulla) which covers the storage chamber. Arrow points to the slit-shaped opening (meatus). b. Longitudinal section through the mesosoma of *A. sexdens,* showing the large region of the metapleural gland (MPG). c. Longitudinal section through metapleural gland: CS = collecting sac; GC = glandular cells; M = meatus; R = storage chamber or receptacle.

Discussion

The metapleural glands have been considered characteristic of all ants with the very few exceptions given by Brown (1968). From a survey of external criteria Brown listed four categories where the metapleural gland appears to be atrophied: "1. Males of army ants, subfamily Dorylinae. 2. Males of a few other genera, mainly in subfamily Myrmicinae (e.g. *Leptothorax duloticus, Tetramorium, Strongylognathus, Rhoptromyrmex, Huberia striata*). 3. Workers of the specialized slave makers of genus *Polyergus*. 4. Queens of certain scattered ant species that are known (or assumed, on grounds of other morphological peculiarities) to be social parasites, i.e., those species which found their colonies in the nests of other ant species". From these findings Brown developed an intriguing hypothesis about the function of the metapleural gland: "the gland produces a substance that, when tasted or smelled, says to another ant colony, especially one of the same species, 'I ám an enemy'." According to Brown's hypothesis "an individual either with the same odor-or-taste, or with none at all, would be treated by its host colony as neutral". This would explain why certain species whose individuals have to enter a foreign colony (social parasites; doryline males) often do not possess a metapleural gland.

This hypothesis was challenged by Maschwitz (Maschwitz et al 1970, Maschwitz 1974). He was unable to experimentally demonstrate an enemy identification effect in the metapleural gland secretions, but he could show that in a number of ant species the metapleural gland secretions serve as powerful antiseptic substances that protect the body surface and nest against microorganisms. For example, the active antibiotic component of *Atta sexdens* was found to be phenylacetic acid, of which one ant stores an average of 1.4 μg (Maschwitz et al 1970). In *Crematogaster* (*Physocrema*) *difformis* the secretions of the enlarged metapleural gland serve as antiseptics, but when discharged in larger quantities they can also repel animal enemies. Finally, in *Crematogaster* (*Physocrema*) *inflata,* which also possesses a hypertrophied metapleural gland, Maschwitz (1974) discovered that the sticky secretions function primarily as an alarm-defense substance. He hypothesized that in this case the antiseptic gland has evolved to become an alarm defense gland.

Our discovery of the atrophy of the metapleural gland among more genera than previously suspected places this organ in a new

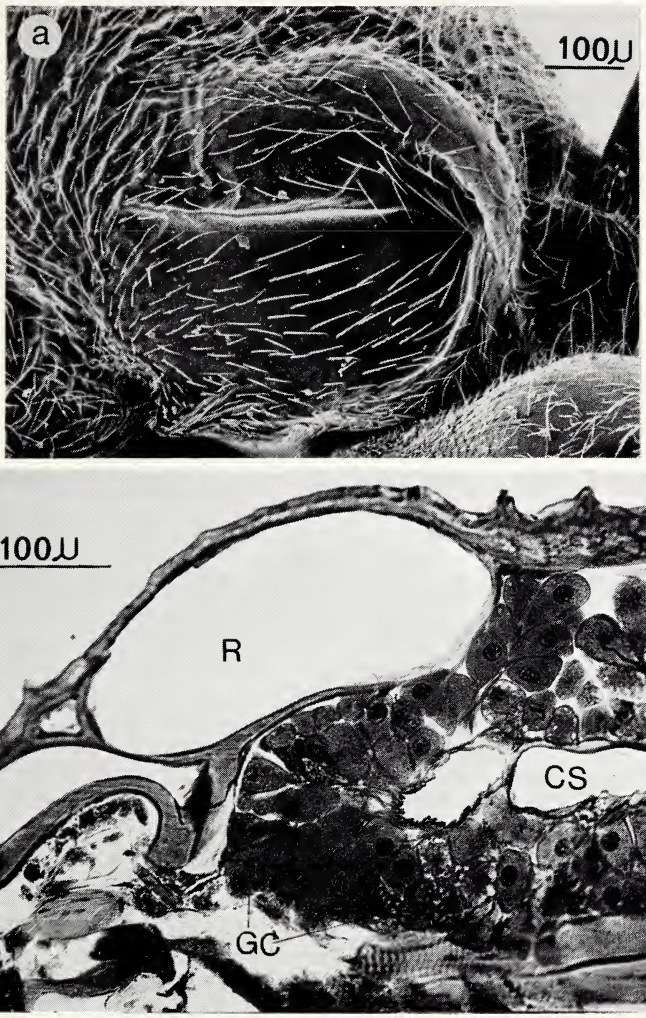


Fig. 2. Metapleural gland of a *Nothomyrmecia macrops* worker. a. SEM micrograph of meatus. b. Longitudinal section through the metapleural gland. CS = collecting sac; GC = glandular cells; R = storage chamber.

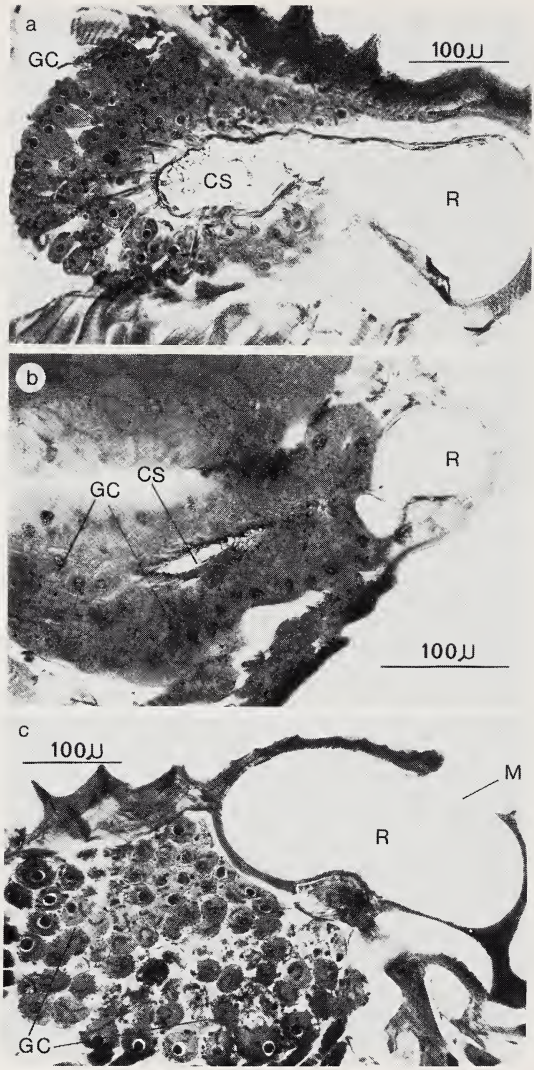
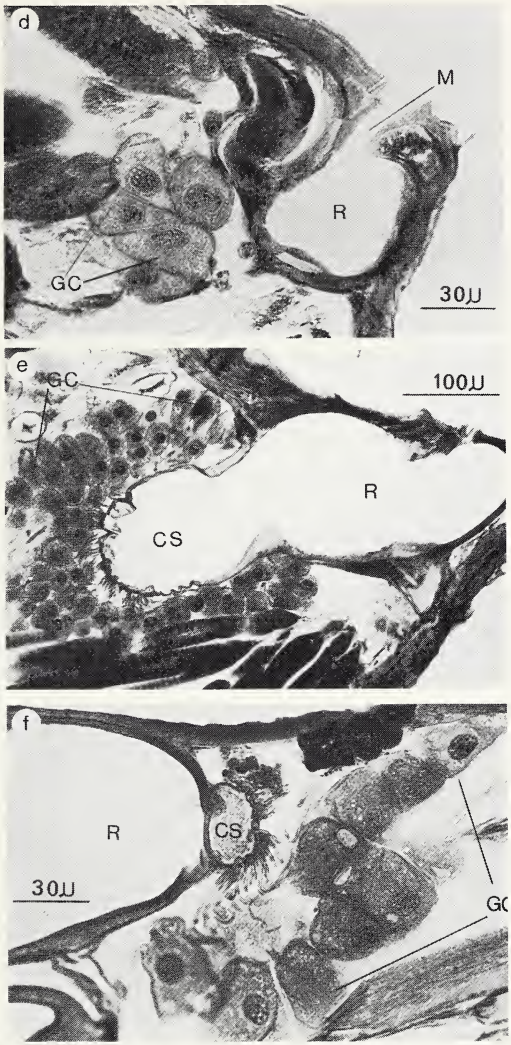


Fig. 3. (Above and facing page) Longitudinal sections through metapleural glands of workers of a. *Myrmecia pilosula;* b. *Cerapachys*? *turneri;* c. *Rhytidoponera metallica;* d. *Pseudomyrmex pallidus;* e. *Novomessor albisetosus;* f. *Myrmecocystus mendax.* CS = collecting sac; GC = glandular cells; R = storage chamber.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light. Since the gland is absent in a number of ant species known to be extremely aggressive and discriminatory towards conspecific foreigners and interspecific competitors (for *Oecophylla* see Hölldobler and Wilson 1978, Hölldobler 1979, 1984; for *Camponotus* see Carlin and Hölldobler 1983) it is obvious that at least in these species the metapleural gland secretions have no function in enemy identification. The absence of the metapleural gland in male ants is also much more widespread than previously assumed. In fact, it appears that species in which males lack this organ or possess it in a very reduced state outnumber those in which the gland is well developed. Most of these males never have to enter a foreign colony in order to mate. Thus Brown's argument concerning the absence of the metapleural gland in doryline males is further weakened.

In our view Maschwitz's experimental evidence concerning the antiseptic effect of most metapleural gland secretions is very convincing. We have repeatedly heard the argument that the secretions of other pheromone glands, such as the mandibular gland or poison gland are also acidic and have the potential of suppressing the growth of *Escherichia coli* in test plates. Thus, it is argued that Maschwitz's tests, although demonstrating an antiseptic effect, do not necessarily prove a primarily antiseptic function of the metapleural gland. Maschwitz himself has pointed out that other exocrine glandular secretions frequently have antiseptic power. In fact, he hypothesized that most epidermal glands originally were antiseptic devices before they became more complex glandular structures that produce either repellent secretions against predators or alarm pheromones used in social communication (Maschwitz 1968, 1974; Maschwitz et al 1970).

Metapleural gland secretions can freely flow out of the storage chamber. The meatus is sometimes densely covered with bristles (Fig. 6), and often there are hairs and dispenser bristles inside the atrium along which the secretion can easily flow to the outer surface (Fig. 6c). As Brown (1968) pointed out, "some ant species have been seen to draw the legs, especially the tibia and tarsi of the forelegs, repeatedly over the meatus of the gland and then rub these leg parts over the rest of the body". In this way the metapleural gland secretion is probably spread over the whole body. It might also be distributed among nestmates by mutual grooming. Thus, it appears

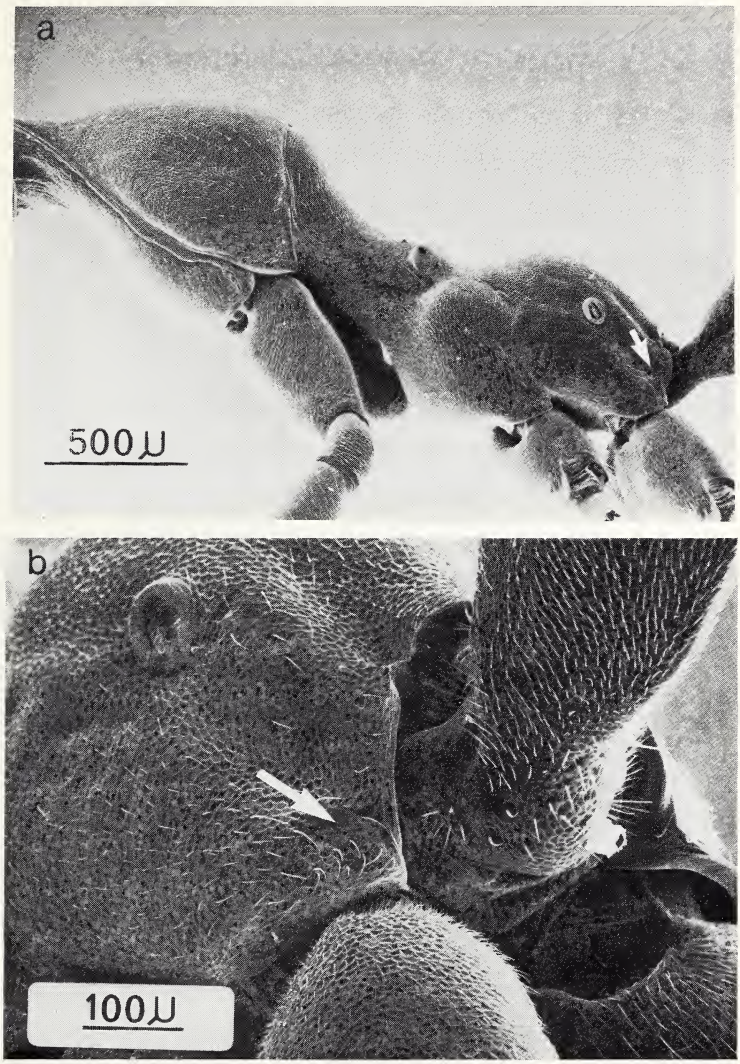


Fig. 4. a. SEM micrograph of the mesosoma of a worker of *Oecophylla longinoda*. b. Close-up of the posterolateral corners of the alitrunk. Arrows indicate the area where the opening of a metapleural gland should be located.

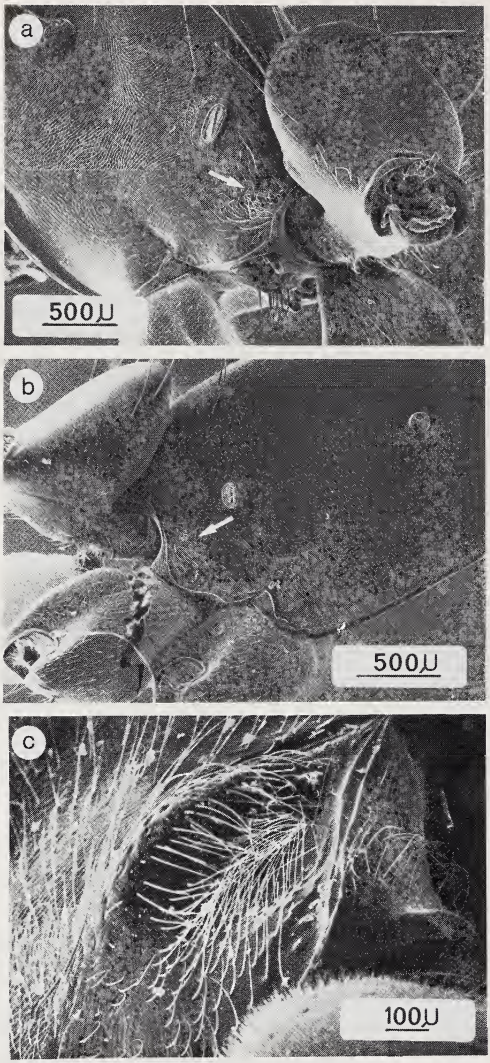
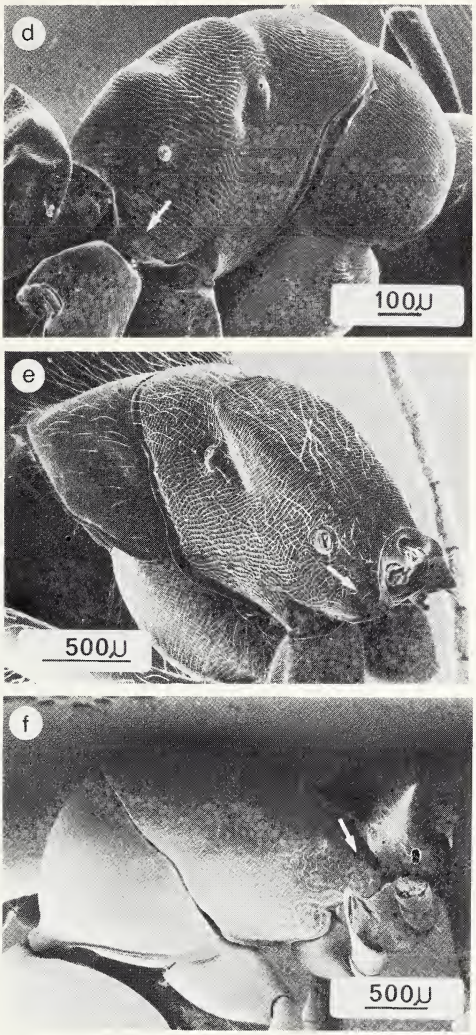


Fig. 5. (Above and facing page) SEM micrographs of the mesosoma of workers of several formicine species. Arrow indicates region where the opening of the metapleural gland should be located. a. *Camponotus pennsylvanicus;* b. *Camponotus consobrinus.* In both species there are clusters of hairs visible in the area of the metapleural gland opening. Both species, however, lack a slit-shaped opening. c. The slit-shaped opening of the metapleural gland of *Camponotus gigas.* No opening can be detected in d. *Colobopsis truncata;* e. *Dendromyrmex chartifex;* f. *Polyrhachis* (*Cyrtomyrma*)? *doddi.*


d
100µ
e
500µ
f
500µ

that the central location and general structure of the metapleural gland makes it ideally suited for distribution of an antiseptic secretion.

Why then is the metapleural gland absent or strongly atrophied in *Oecophylla, Polyrhachis, Dendromyrmex,* most *Camponotus,* certain social parasitic ants, and many male ants? Maschwitz et al (1970) offered the following explanations for the last two cases. Social parasitic ants, they argued, are usually highly attractive to the host ants, which groom them very frequently, so that the social parasites benefit from the social distribution of the antiseptic secretions of their host ants. This relieves the parasitic species of the burden of producing their own antiseptics and allows them to deploy the freed energy into other organs and functions. The absence of metapleural glands in male ants was given a different adaptive significance. Males live only a relatively short time inside the nest. They are also much less numerous than workers. Therefore, there exists no particular need for them to produce large amounts of antiseptic secretions.

The latter hypothesis, of course, raises the question why in some species the males do have relatively large metapleural glands (Fig. 7f, Tab. 1). The reason could be that in those cases the ratio of males to workers might be much higher and/or the males might reside inside the nest for longer periods and therefore would present a considerable "antiseptic burden" to the colony. This would favor the selection of males capable of producing their own antiseptic secretions. Furthermore, the metapleural gland of male ants could also have another, secondary function, which does not exclude the primary antiseptic function; that is, it could produce sex pheromones and hence be an important character maintained by sexual selection. During mating females might thus favor males with well developed metapleural glands, and the capacity to produce larger quantities of pheromone.

It is interesting that in all weaver ant species studied the metapleural gland was atrophied. The species we checked included *Oecophylla, Polyrhachis* (*Cyrtomyrma*)? *doddi, Dendromyrmex, Camponotus xenex.* It is reasonable to speculate that these arboreal ants are much less exposed to microorganisms than terrestrial ant species, and therefore an antiseptic metapleural gland became unnecessary.

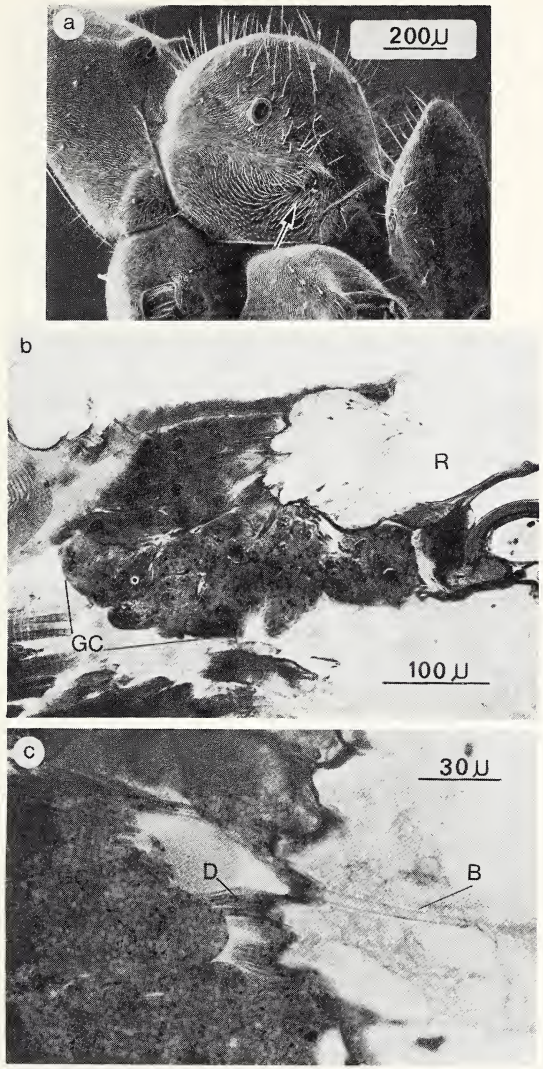


Fig. 6. The metapleural gland of a worker of *Iridomyrmex purpureus* a. SEM micrograph of mesosoma. The arrow points to the opening of the metapleural gland. b. Longitudinal section through the metapleural gland. c. Close-up of a section through the glandular cells (GC) and dispenser bristles (B); D = glandular duct; R = collecting chamber.

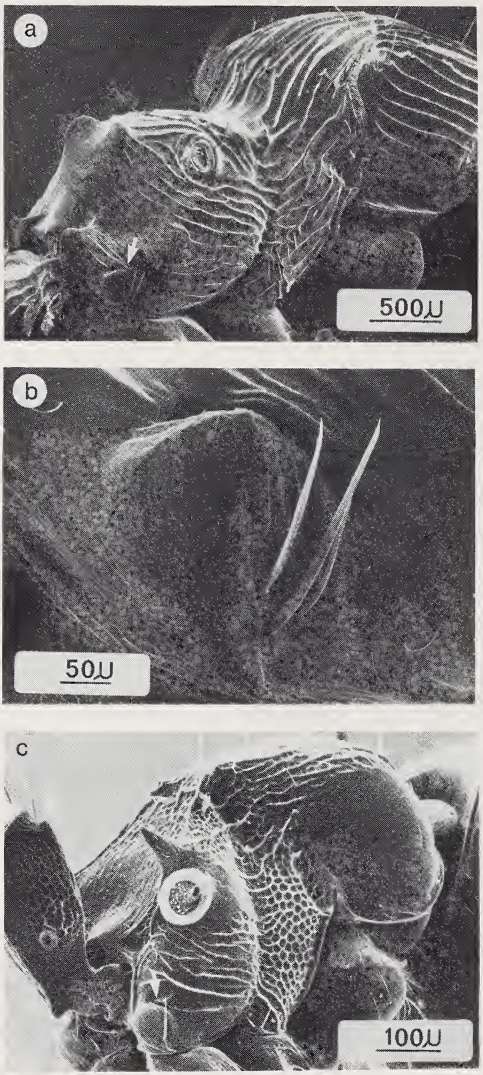


Fig. 7. (Above and facing page) SEM micrographs of the exterior structures of the metapleural glands of several ant species. a. Alitrunk of *Podomyrma pulchra* worker. b. Close-up of bulla, slit-shaped opening and sensory hairs (?) of the metapleural gland of *P. pulchra* worker. c. Alitrunk of *Crematogaster* sp 10 (ANIC) worker. d. Alitrunk of *Catalacus intrudens* worker. e. metapleural gland opening with sensory hairs (?) of *C. intrudens* worker. f. Alitrunk of *Crematogaster* sp 10 (ANIC) male. Arrows point to the opening of the metapleural gland.

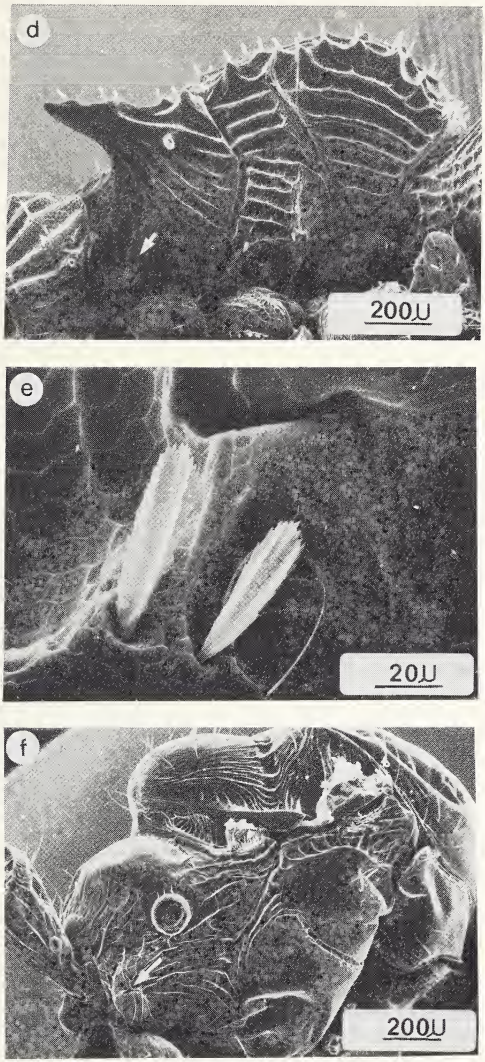

d
200µ
e
20µ
f
200µ

Table 1. Evaluation of the histological preparations of the metapleural glands of ants. Species which could not be identified with certainty are listed either by the accession number of our histological collection, or by the species number assigned by the Australian National Insect Collection (ANIC), where voucher specimens have been deposited.

subfamily/species	collector and locality	metapleural gland present (+), absent (−), and approximate number of cells in worker	queen	male
MYRMECIINAE				
Myrmecia pilosula	B. Hölldobler, NSW, Australia	+ (239)		−
PONERINAE				
Amblyopone australis	B. Hölldobler, Canberra, Australia	+ (75)		
Amblyopone pallipes	J. Traniello, Massachusetts, USA	+ (58)		
Amblyopone reclinata	B. B. Lowery, Corregidor Isl. Philippine Rep.	+ (32)		
Cerapachys ? *turneri*	B. Hölldobler, Eungella, Queensland, Australia	+ (97)		
Hypoponera sp. 3 (ANIC)	B. Hölldobler, Eungella, Queensland, Australia	+ (38)		−
Leptogenys diminuta	B. Hölldobler, Kuranda, Queensland, Australia	+ (137)		−
Leptogenys nitida	B. Hölldobler, Shimba Hills, Kenya	+ (85)		
Leptogenys regis	B. Hölldobler, Shimba Hills, Kenya	+ (98)		

Myopopone castanea	P. J. Greenslade, Solomon Islands	+ (241)		
Mystrium camillae	R. W. Taylor, Mt. Santubang, Borneo	+ (47)		
Onychomyrmex hedleyi	R. W. Taylor, B. Hölldobler, L. Eacham, Qld, Australia	+ (36)	+ (102)	
Onychomyrmex doddi	P. Ward, Lake Eacham, Qld., Australia	+ (27)		
Onychomyrmex sp. 2 (ANIC)	R. W. Taylor, B. Hölldobler, L. Eacham, Qld., Australia	+ (45)		
Onychomyrmex sp. 1 (ANIC)	R. W. Taylor, Mt. Lewis, Qld., Australia	+ (33)		
Pachycondyla crassa	B. Hölldobler, Shimba Hills, Kenya	+ (107)		
Pachycondyla obscuricornis	J. Traniello, BCI, Panama	+ (128)		−
Rhytidoponera metallica	C. P. Haskins, Sydney, NSW, Australia	+ (135)		−
Sphinctomyrmex steinheili	B. Hölldobler, Canberra, Australia	+ (76)		
DORYLINAE				
Eciton hamatum	R. Silberglied, BCI, Panama	worker: + (120) soldier: + (180)		−
Neivamyrmex nigrescens	B. Hölldobler, Portal, Arizona, USA	+ (201)		−

Table 1. Evaluation of the histological preparations of the metapleural glands of ants. Species which could not be identified with certainty are listed either by the accession number of our histological collection, or by the species number assigned by the Australian National Insect Collection (ANIC), where voucher specimens have been deposited

subfamily/species	collector and locality	metapleural gland present (+), absent (−), and approximate number of cells in worker	queen	male
MYRMECIINAE				
Myrmecia pilosula	B. Hölldobler, NSW, Australia	+ (239)		−
PONERINAE				
Amblyopone australis	B. Hölldobler, Canberra, Australia	+ (75)		
Amblyopone pallipes	J. Traniello, Massachusetts, USA	+ (58)		
Amblyopone reclinata	B. B. Lowery, Corregidor Isl. Philippine Rep.	+ (32)		
Cerapachys ? turneri	B. Hölldobler, Eungella, Queensland, Australia	+ (97)		
Hypoponera sp. 3 (ANIC)	B. Hölldobler, Eungella, Queensland, Australia	+ (38)		−
Leptogenys diminuta	B. Hölldobler, Kuranda, Queensland, Australia	+ (137)		−
Leptogenys nitida	B. Hölldobler, Shimba Hills, Kenya	+ (85)		
Leptogenys regis	B. Hölldobler, Shimba Hills, Kenya	+ (98)		
Myopopone castanea	P. J. Greenslade, Solomon Islands	+ (241)		
Mystrium camillae	R. W. Taylor, Mt. Santubang, Borneo	+ (47)		
Onychomyrmex hedleyi	R. W. Taylor, B. Hölldobler, L. Eacham, Qld, Australia	+ (36)	+ (102)	
Onychomyrmex doddi	P. Ward, Lake Eacham, Qld., Australia	+ (27)		
Onychomyrmex sp. 2 (ANIC)	R. W. Taylor, B. Hölldobler, L. Eacham, Qld., Australia	+ (45)		
Onychomyrmex sp. 1 (ANIC)	R. W. Taylor, Mt. Lewis, Qld., Australia	+ (33)		
Pachycondyla crassa	B. Hölldobler, Shimba Hills, Kenya	+ (107)		
Pachycondyla obscuricornis	J. Traniello, BCI, Panama	+ (128)		−
Rhytidoponera metallica	C. P. Haskins, Sydney, NSW, Australia	+ (135)		−
Sphinctomyrmex steinheili	B. Hölldobler, Canberra, Australia	+ (76)		
DORYLINAE				
Eciton hamatum	R. Silberglied, BCI, Panama	worker: + (120) soldier: + (180)		−
Neivamyrmex nigrescens	B. Hölldobler, Portal, Arizona, USA	+ (201)		−

Table 1. (Continued) Evaluation of the histological preparations of the metapleural glands of ants. Species which could not be identified with certainty are listed either by the accession number of our histological collection, or by the species number assigned by the Australian National Insect Collection (ANIC), where voucher specimens have been deposited.

subfamily/species	collector and locality	metapleural gland present (+), absent (−), and approximate number of cells in worker	queen	male
PSEUDOMYRMECINAE				
Pseudomyrmex ferruginea	R. Silberglied, Cerro Gallera, Panama	+ (65)		
Pseudomyrmex pallidus	P. Ward, Mustang Is., Texas, USA	+ (35)		−
MYRMICINAE				
Aphaenogaster rugis	J. Traniello, Concord, Mass., USA	+ (180)		
Atta sexdens	N. Weber, Guyana	media: + (473)		
Catalacus intrudens	B. Hölldobler, Shimba Hills, Kenya	+ (?)		−
Daceton armigerum	E. O. Wilson, Fazenda Esteio, Brazil,	+ (70)		
Leptothorax alardycei	B. Cole, Keys, Florida, USA	+ (85)		+ (40)
Myrmica americana	J. Traniello, Massachusetts, USA	+ (150)		
Novomessor albisetosus	B. Hölldobler, Portal, Arizona, USA	+ (250)		
Novomessor cockerelli	B. Hölldobler, Portal, Arizona, USA	+ (272)		+ (62)

Orectognathus versicolor	B. Hölldobler, Eungella, Qld., Australia	minor: + (87) media: + (79) major: + (89)		–
Pheidole embolopyx	E. O. Wilson, Fazenda Esteio, Brazil	soldier: + (31)	+ (65)	
Pogonomyrmex badius	B. Hölldobler, Tampa, Florida, USA	+ (242)		
Solenopsis fugax	B. Hölldobler, Gerbrunn, Bavaria, Germany	+ (82)	+ (178)	
Veromessor pergandei	G. Alpert, Tucson, Arizona, USA	+ (210)		
NOTHOMYRMECIINAE				
Nothomyrmecia macrops	R. W. Taylor, Poochera, S. Australia	+ (272)	+ (439)	–
ANEURETINAE				
Aneuretus simoni	A. Jayasuriya, Sri Lanka	+ (14)		–
DOLICHODERINAE				
Iridomyrmex purpureus	B. Hölldobler, Canberra, Australia,	+ (317)		+ (190)
Conomyrma bicolor	B. Hölldobler, Arizona, USA	+ (125)		
FORMICINAE				
Camponotus consobrinus	B. Hölldobler, Canberra, Australia	–	–	
Camponotus ligniperda	B. Hölldobler, Ochsenfurt, Bavaria, Germany	–	–	–

Table 1. (Continued) Evaluation of the histological preparations of the metapleural glands of ants. Species which could not be identified with certainty are listed either by the accession number of our histological collection, or by the species number assigned by the Australian National Insect Collection (ANIC), where voucher specimens have been deposited.

subfamily species	collector and locality	metapleural gland present (+), absent (−), and approximate number of cells in worker	queen	male
PSEUDOMYRMECINAE				
Pseudomyrmex ferruginea	R. Silberglied, Cerro Gallera, Panama	+ (65)		
Pseudomyrmex pallidus	P. Ward, Mustang Is., Texas, USA	+ (35)		−
MYRMICINAE				
Aphaenogaster rugis	J. Traniello, Concord, Mass., USA	+ (180)		
Atta sexdens	N. Weber, Guyana	media: + (473)		
Catalaucus intrudens	B. Holldobler, Shimba Hills, Kenya	+ (?)		−
Daceton armigerum	E. O. Wilson, Fazenda Esteio, Brazil,	+ (70)		
Leptothorax alardycei	B. Cole, Keys, Florida, USA	+ (85)		+ (40)
Myrmica americana	J. Traniello, Massachusetts, USA	+ (150)		
Novomessor albisetosus	B. Holldobler, Portal, Arizona, USA	+ (250)		
Novomessor cockerelli	B. Holldobler, Portal, Arizona, USA	+ (272)		+ (62)

Orectognathus versicolor	B. Holldobler, Eungella, Qld., Australia	minor + (87) media: + (79) major: + (89)		−
Pheidole embolopyx	E. O. Wilson, Fazenda Esteio, Brazil	soldier: + (31)	+ (65)	
Pogonomyrmex badius	B. Holldobler, Tampa, Florida, USA	+ (242)		
Sclenopsis fugax	B. Holldobler, Gerbrunn, Bavaria, Germany	+ (82)	+ (178)	
Veromessor pergandei	G. Alpert, Tucson, Arizona, USA	+ (210)		
NOTHOMYRMECINAE				
Nothomyrmecia macrops	R. W. Taylor, Poochera, S. Australia	+ (272)	+ (439)	−
ANEURETINAE				
Aneuretus simoni	A. Jayasuriya, Sri Lanka	+ (14)		−
DOLICHODERINAE				
Iridomyrmex purpureus	B. Holldobler, Canberra, Australia,	+ (317)		+ (190)
Conomyrma bicolor	B. Holldobler, Arizona, USA	+ (125)		
FORMICINAE				
Camponotus consobrinus	B. Holldobler, Canberra, Australia	−	−	
Camponotus ligniperda	B. Holldobler, Ochsenfurt, Bavaria, Germany	−	−	−

Table 1. (Continued) Evaluation of the histological preparations of the metapleural glands of ants. Species which could not be identified with certainty are listed either by the accession number of our histological collection, or by the species number assigned by the Australian National Insect Collection (ANIC), where voucher specimens have been deposited.

subfamily/species	collector and locality	metapleural gland present (+), absent (−), and approximate number of cells in worker	queen	male
Camponotus pennsylvanicus	N. Carlin, Blue Hills, Massachusetts, USA	−		
Dendromyrmex chariflex	J. Wenzel, BCI, Panama	−		
Formica perpilosa	B. Hölldobler, Arizona, USA	+ (60)		+ (23)
Formica rufibarbis	B. Hölldobler, Würzburg, Bavaria, Germany	+ (52)		
Myrmecocystus mendax	B. Hölldobler, Portal, Arizona, USA	+ (65)		
Myrmecocystus mexicanus	B. Hölldobler, Portal, Arizona, USA	+ (73)		
Myrmecocystus mimicus	B. Hölldobler, Portal, Arizona, USA	+ (79)		+ (22)
Oecophylla longinoda	B. Hölldobler, Shimba Hills, Kenya,	−	−	−
Oecphylla smaragdina	B. Hölldobler, Port Douglas, Qld, Australia	−		
Polyergus rufescens	B. Hölldobler, Gerbrunn, Bavaria, Germany	−		
Polyrhachis (*Cyrtomyrma*) ? *doddi*	B. Hölldobler, Port Douglas, Qld, Australia	−	−	−

Table 2. An external survey of the presence (+) or absence (−) of features that indicate a metapleural gland in the genera *Camponotus, Dendromyrmex,* and *Polyrhachis.* Further information concerning species identification see Table 1.

species	collector and locality	metapleural gland
Camponotus abdominalis floridanus	N. Carlin, Sugarloaf Key, Florida USA	−
C. ? *aeneopilosus* (sp. 3, ANIC)	B. Hölldobler, Canberra, Australia	−
C. americanus	N. Carlin, Blue Hills, Massachusetts, USA	−
C. castaneus	P. Calabi, Tall Timbers, Florida, USA	−
C. ? *ephippium* (sp. 13, ANIC)	B. Hölldobler, Canberra, Australia	−
C. ferrugineus	N. Carlin, Blue Hills, Massachusetts, USA	−
C. gigas	?, S-Sumatra	+
C. herculeanus	B. Hölldobler, Gramschatz, Bavaria, Germany	−
C. ? *intrepidus* (sp. 4, ANIC)	B. Hölldobler, Canberra, Australia	−
C. midas (acc. #190)	B. Hölldobler, Poochera, Australia	−
C. nearcticus	N. Carlin, Blue Hills, Massachusetts, USA	−
C. ? *nigriceps* (sp. 2, ANIC)	B. Hölldobler, Poochera, Australia	−
C. perthiana	B. Hölldobler, Canberra, Australia	−
C. planatus	B. Hölldobler, Keys, Florida, USA	−
C. schaeferi	M. Möglich, Portal, Arizona, USA	−
C. senex	W. M. Wheeler, Pueblo Nuervo, Panama	−
C. sericeiventris	J. Traniello, BCI, Panama	−
C. socius	B. Hölldobler, Tampa, Florida, USA	−
C. ? *suffusus* (acc. #236)	B. Hölldobler, Canberra, Australia	−
C. tortuganus	N. Carlin, Sugarloaf Key, Florida	−

Table 2. (Continued) An external survey of the presence (+) or absence (−) of features that indicate a metapleural gland in the genera *Camponotus, Dendromyrmex,* and *Polyrhachis.* Further information concerning species identification see Table 1.

species	collector and locality	metapleural gland
C. vicinus	N. Carlin, N. Franks, Cortez, Colorado, USA	−
C. sp. 10 (ANIC)	B. Hölldobler, Poochera, S. Australia	−
C. sp. 14 (ANIC)	B. Hölldobler, Canberra, Australia	−
C. sp. 19 (ANIC) (walkeri group)	B. Hölldobler, Cooktown, Qld, Australia	−
C. sp. 20 (ANIC)	B. Hölldobler, Canberra, Australia	−
C. sp. 21 (ANIC)	B. Hölldobler, Kuranda, Australia	−
C. sp. 22 (ANIC) (clareipes group)	B. Hölldobler, Bateman's Bay, NSW, Australia	−
Dendromyrmex fabricii	J. Wenzel, BCI, Panama	−
Polyrhachis ? *ammon* (acc. #65)	B. Hölldobler, Bateman's Bay, NSW, Australia	−
P. ? *gab* (acc. #102)	B. Hölldobler, Mt. Carbine, Qld, Australia	−
P. schlueteri	B. Hölldobler, Shimba Hills, Kenya	−
P. ? *sokolova* (acc. #95)	B. Hölldobler, Port Douglas, Qld, Australia	−
P. sp. 2 (ANIC)	B. Hölldobler, Canberra, Australia	−
P. sp. 3 (ANIC)	B. Hölldobler, Canberra, Australia	−

On the other hand other arboreal species, such as *Pseudomyrmex, Podomyrma, Catalaucus* (Fig. 7), *Opisthopsis respiciens,* and *Lasius fuliginosus* have well-developed metapleural glands, whereas some terrestrial *Polyrhachis* and *Camponotus* have lost their metapleural gland. But this does not contradict our speculation. An arboreal life style might favor but not necessitate a reduction and atrophy of the metapleural gland.* Furthermore, most *Camponotus* and *Polyrhachis* species are arboreal or live in or

*In a similar manner, the social parasitic life style appears to favor but does not necessitate the reduction of the metapleural gland (see Maschwitz et al 1970).

on large pieces of dead wood. It is entirely possible that contemporary terrestrial species might have originiated from arboreal ancestors that had already lost their metapleural gland. We have currently no explanation, however, why *Camponotus gigas* appears to have retained or redeveloped its metapleural gland. Of course, it would also be interesting to known how those terrestrial species that have lost their metapleural gland defend themselves and their nests against microbial and fungal attacks.

Acknowledgements

We thank all the collectors mentioned in Table 1 and 2, and B. Bolton, W. L. Brown, R. Snelling, R. W. Taylor for helping us with the identification of many species, and Ed Seling for his assistance during the SEM work. Special thanks to R. W. Taylor and the Division of Entomology, CSIRO, Canberra (Australia) who in many ways supported this study. The work was further supported by grants from the National Science Foundation, the National Geographic Society and the John Simon Guggenheim Foundation.

Appendix

We would like to take this opportunity to correct some errors which appeared in two of our previous publications on exocrine glands in ants.

1) In our paper "Tergal and sternal glands in ants" (Psyche *85,* 285–330, 1978) on page 297, (Table 1a), Myrmecinae should be corrected to Myrmicinae; on page 298, the locality of *Veromessor pergandei,* given as Mexico, should be corrected to Arizona; on page 299, the species *Pachycondyla* spec. listed under the subfamily Formicinae should be corrected to *Acantholepis* spec.

2) In our paper "Tergal and sternal glands in male ants" (Psyche *89,* 113–132, 1982), Fig 1B, the lettering PG should be changed to P, because it indicates part of the penis with the penis gland, and not the pygidial gland (PG), shown in Fig. 1A.

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A NEW EXOCRINE GLAND IN THE SLAVE RAIDING ANT GENUS *POLYERGUS*

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Introduction

In his classical study of the workers and males of *Myrmica rubra,* Janet (1898, 1901) discovered a pair of clusters of a few glandular cells under the 6th abdominal tergite. Each cell is drained by a duct that penetrates the intersegmental membrane between the 6th and 7th abdominal tergites. Recent investigations have demonstrated that this gland is very common in ants, but it varies considerably in size and structure (Hölldobler and Engel 1978). Since the gland is anatomically closely associated with the last exposed tergite in female ants (7th abdominal tergite = pygidium) Kugler (1978) suggested that it be called the *pygidial gland.* Recently Jessen and Maschwitz (1983) proposed the alternative name, *Janet's gland,* in honor of its discoverer Charles Janet.

The pygidial gland has been found in workers of representative species belonging to all subfamilies except the Formicinae (for literature review see Hölldobler and Engel 1978; Hölldobler and Engel-Siegel 1982; Hölldobler 1982).

I report here the first discovery of a pygidial gland in *Polyergus,* a genus of the subfamily Formicinae. But the anatomy has unusual features that point to a possibly indepedent origin in evolution.

Material and Methods

Three species of *Polyergus* were investigated. The European species *Polyergus rufescens* was collected near Würzburg (W-Germany), the two North American species *P. breviceps* and *P. lucidus* were found near Portal (Arizona) and near Rocky Point in Suffolk County (New York), respectively. Virgin queens and males were

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available only in the case of *P. lucidus*. For comparison two common slave species of *P. rufescens, Formica rufibarbis* and *F. fusca* (from the Würzburg area), as well as two species of the slave raiding *Formica sanguinea* group (collected in Massachusetts), were also studied.

For histological investigations life specimens were fixed in alcoholic Bouin or Carnoy (Romeis 1948), embedded in methylmethacrylate, and sectioned 6–8 μ thick with a D-profile steel knife on a Jung Tetrander I microtome (Rathmayer 1962). The staining was Azan (Heidenhain). The SEM pictures were taken with an AMR 1000 A scanning electron microscope.

Results

Workers and queens of the three *Polyergus* species investigated possess a large, tergal complex gland. One part of it is located between the 6th and 7th abdominal tergites; the other part belongs to the 7th tergite (Fig. 1). Because of its anatomical location I propose tentatively to call this organ pygidial gland, although it differs in several respects from the pygidial glands found in other ant subfamilies.

The pygidial gland of *Polyergus* consists of a reservoir, formed by an invagination of the intersegmental membrane between 6th and 7th abdominal tergites. Glandular cells (~80 cells in *P. rufescens* workers) are drained into this reservoir through ducts penetrating the intersegmental membrane. Ducts of a second group of glandular cells open into a series of cuticular cups located along the anterior margin of the 7th abdominal tergite (Fig. 1, 2). This striking cuticular structure is usually not visible, because it is covered by the posterior portion of the 6th abdominal tergite. It is, however, easily exposed by slightly pulling the two terminal abdominal tergites apart. Although only a few specimens of each species were investigated in detail, species-specific differences in the pygidial cup structure are so conspicuous that this organ might be considered a valid taxonomic character.

The cup structure is most strikingly developed in workers of *P. rufescens* (Fig. 2). In this case several cups are often merged to form one large cup containing 2–5 glandular cell openings. I counted a total of approximately 250 duct openings on the pygidium of *P. rufescens* workers. In workers of *P. breviceps* the cup structure is

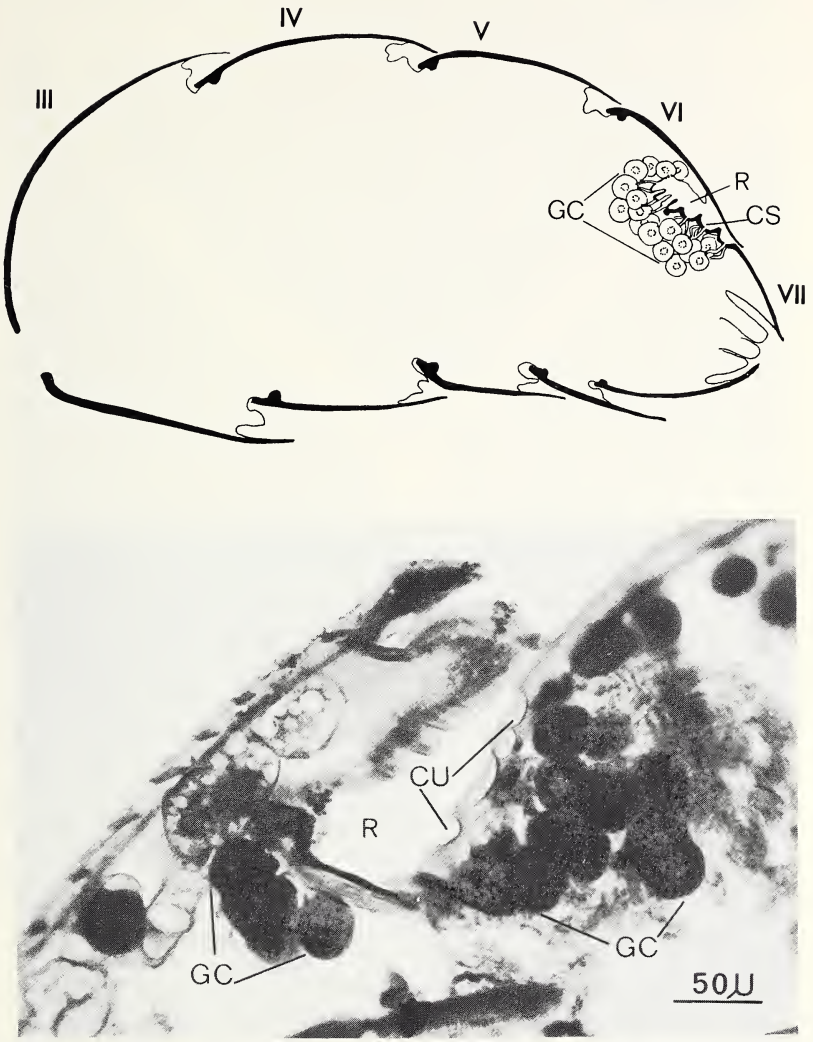

Fig. 1. Above: Schematical illustration of the *Polyergus* pygidial gland between 6th and 7th abdominal tergites. Below: Longitudinal section through the pygidial gland of a *P. rufescens* worker. CS: cup structure; CU: cup; GC: glandular cells; R: intersegmental reservoir.

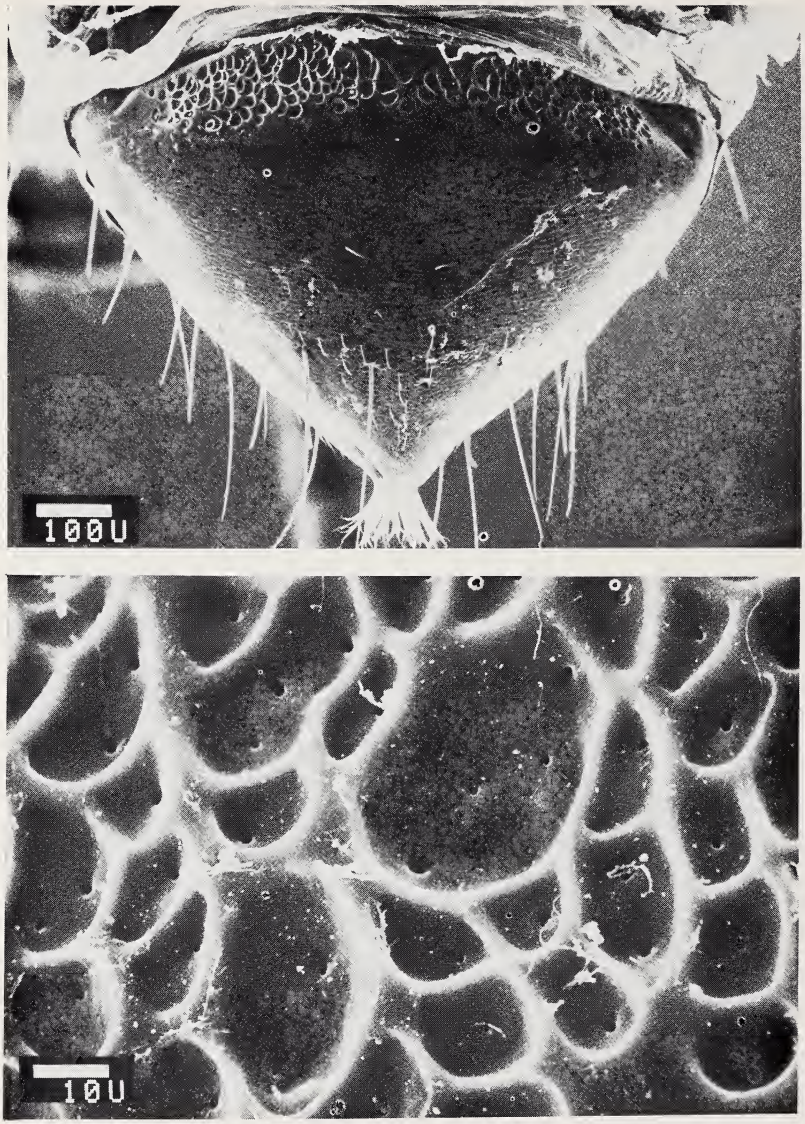

Fig. 2. SEM-photographs of the pygidial cup structure of a *P. rufescens* worker. Above: overview of the pygidium (= 7th abdominal tergite). Below: close-up of the cup structure. Note the duct openings inside the cups.

smaller (with a total of ~150 duct openings), but in this species as well several small cups frequently form one large cup (Fig. 3). In *P. lucidus* workers the pygidial cup structure is still smaller, with approximately 100 duct openings. In this case the cup structure consists primarily of single cups (Fig. 4). It is interesting to note, however, that in *P. lucidus* queens the pygidial cup structure is considerably larger (~200 duct openings), and many of the cups are merged (Fig. 5).

External morphological studies of *P. lucidus* males indicate that they lack the organ.

Formica rufibarbis and *F. fusca,* two common slave species of *P. rufescens,* as well as two representatives of the slave raiding *Formica sanguinea* group were found not to possess a pygidial gland (Fig. 6).

Discussion

Of a total of 17 formicine species investigated (the current study and Hölldobler and Engel 1978) belonging to 6 genera (*Acantholepis, Camponotus, Formica, Myrmecocystus, Oecophylla, Polyergus*) only those in *Polyergus* possess the pygidial gland. This structure is a complex gland with one group of glandular cells opening into an intersegmental reservoir, and another group of cells being drained into cuticular cups in the 7th abdominal tergite. From these features and from its general anatomy I conclude that the pygidial gland of *Polyergus* is not homologous with the pygidial gland of other ant subfamilies, but has evolved independently, possibly in connection with the highly specialized slave raiding behavior of *Polyergus.*

Polyergus slave raids are organized by scout ants that deposit chemical trails (Talbot 1967). The precise origin of the trail pheromones has not yet been established. In most formicine species secretions from the rectal bladder serve as trail pheromones (for review see Hölldobler 1978). These function in many cases primarily as orientation cues and are often supplemented by excitement (or arousal) signals, which can be chemical or mechanical in nature. Recent observations suggest that recruitment to slave raids in *Polyergus* might be based on a similar mechanism.

Topoff et al. (1984) found that individual scout ants lead the raiding party of nestmates to the slave ants' nest. He observed that the ants, although following a chemical trail, tend to "swarm"

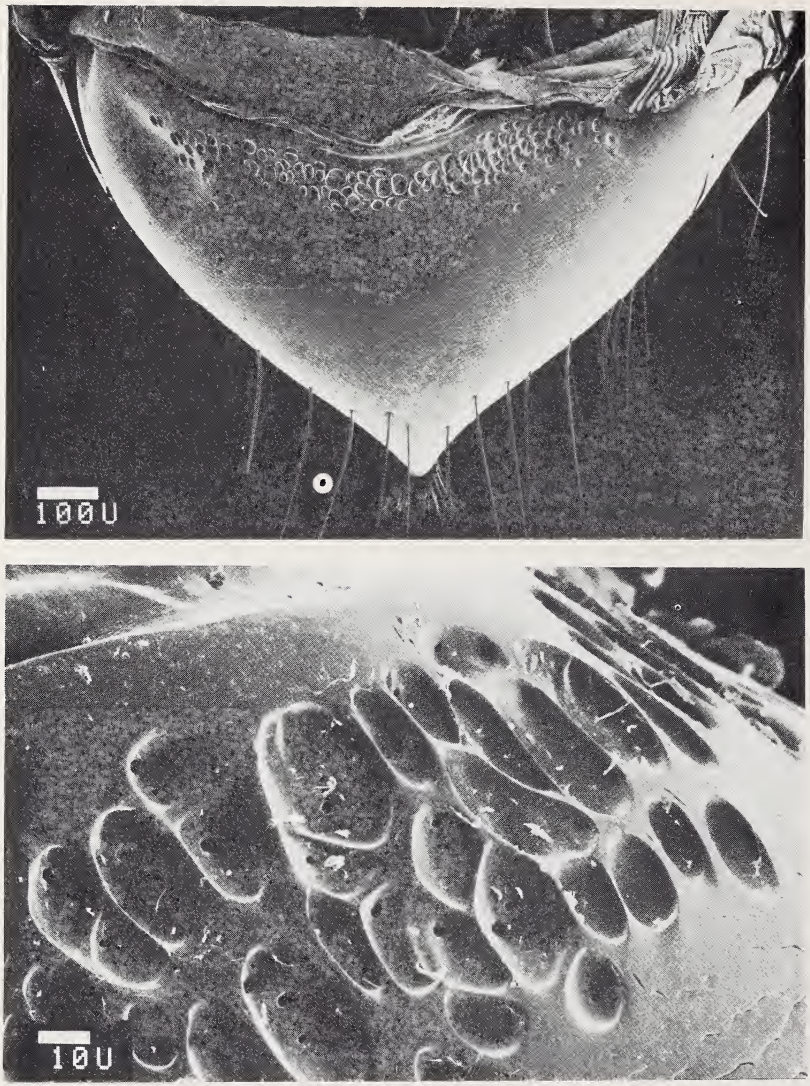

Fig. 3. SEM-photograph of the pygidial cup structure of a *P. breviceps* worker. Above: overview of the pygidium. Below: close-up of the cup structure.

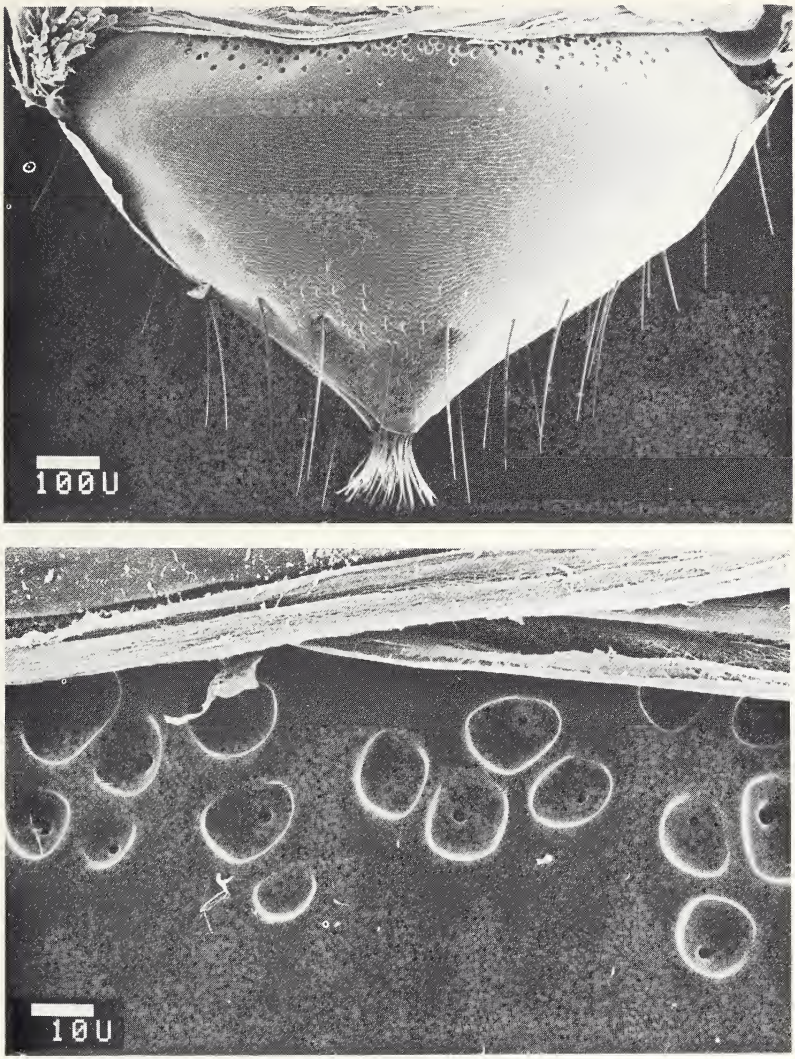

Fig. 4. SEM-photograph of the pygidial cup structure of a *P. lucidus* worker. Above: overview of the pygidium. Below: close-up of cup structure.

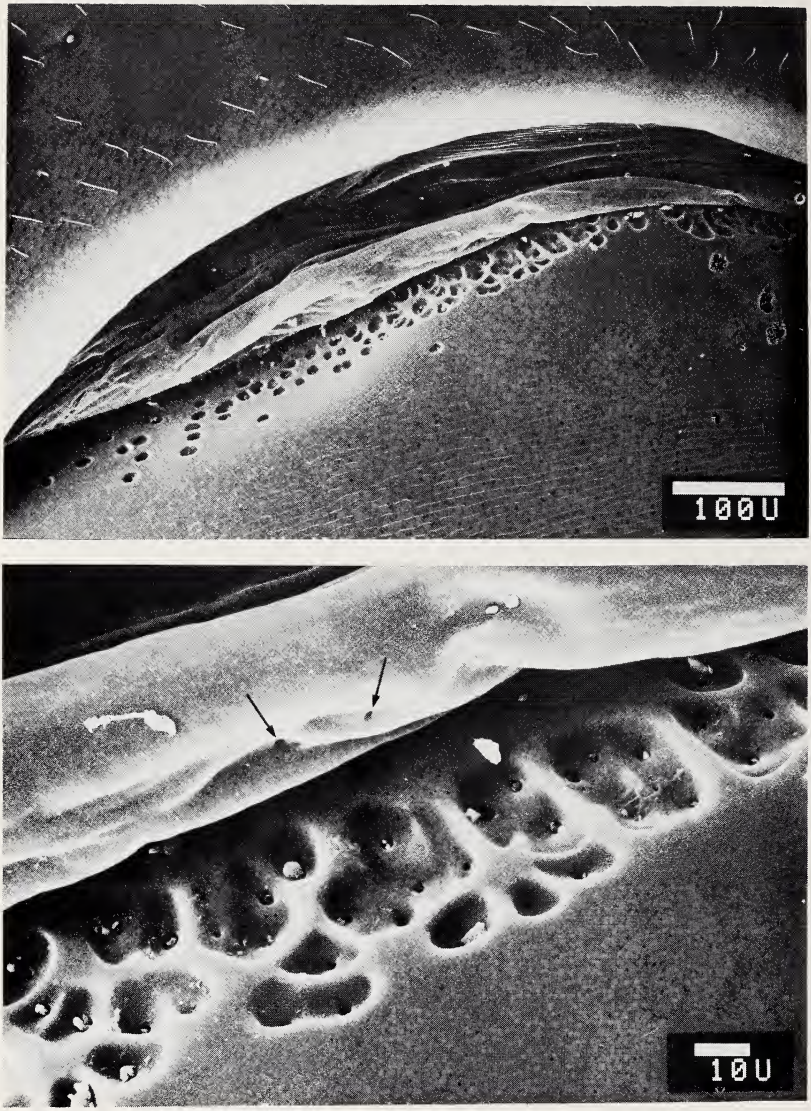

Fig. 5. SEM-photograph of the pygidial cup structure of a *P. lucidus* queen. Above: overview of the cup structure at the anterior margin of the 7th abdominal tergite. Below: close-up of the cup structure. Arrows point ot the intersegmental duct openings.

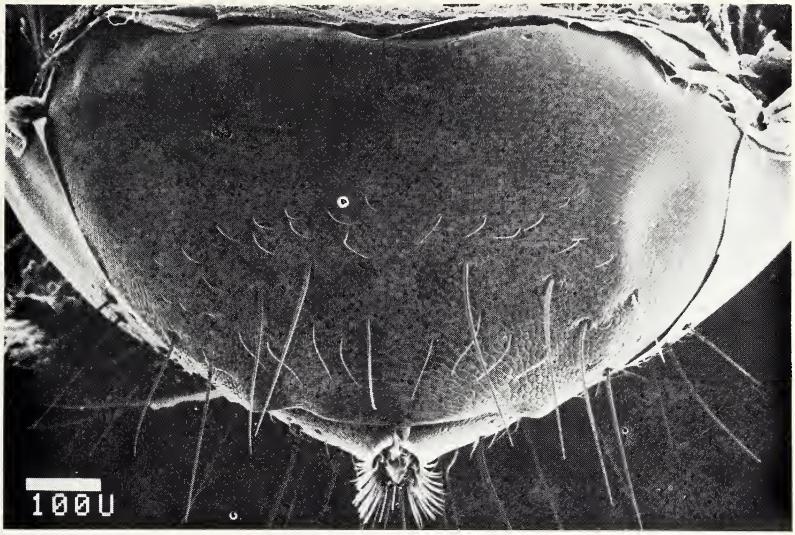

Fig. 6. SEM-photograph of the pygidium of a worker belonging to the *Formica sanguinea* group. Note: no cup structure on the anterior margin of the 7th abdominal tergite.

around the leader ant, often moving briefly ahead, but always returning to the leader. Myrmecologists have long noted this peculiar looping behavior at the front of the raiding columns of *Polyergus* (see for example Schmitz 1906), but only the recent studies by Topoff have indicated that this appears to be due to the orgainizing role and excitement emanating from the leader ant. These observations suggest that the leader discharges not only a longer lasting trail pheromone but also an arousal signal, possibly from the pygidial gland.

Similar recruitment patterns have been observed in *Camponotus socius* and *Myrmecocystus mimicus,* where secretions from the poison gland seem to function as arousal signals (Hölldobler 1971, 1981), as well as in *Camponotus ephippium,* where the arousal signal appears to originate from the cloacal gland (Hölldobler 1982).

However, this hypothesis cannot be applied to the well developed pygidial gland in *Polyergus* queens. Wasmann (1915) first proposed that a young *Polyergus* queen, in order to found a new colony, has to intrude a colony of a slave ant species, where she kills the resident

queen and is subsequently adopted as the "replacement" queen by the slave ant workers. This mode of parasitic colony founding was later confirmed in field observations by Gösswald (1932).

It is possible that the *Polyergus* queen achieves her acceptance in the foreign colony by emitting either a supernormal attractant or a disorganizing alarm substance (hence, some form of queen "propaganda" substance), possibly discharged from the pygidial gland. In fact, the pygidial gland secretions of *Polyergus* workers might also function as a kind of propaganda allomone when encountered by slave ants, very similar to the Dufour's gland secretions of the slave raiding species *Formica pergandei* and *Formica subintegra* which have a confusing propaganda effect on the raided slave ant colony (Regnier and Wilson 1971).

Further experimental work is required to determine which, if any, of these proposed speculations on the function of the *Polyergus* pygidial gland is correct.

Acknowledgements

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COLONY COMPOSITION IN FOUR SPECIES OF POLISTINAE FROM SURINAME, WITH A DESCRIPTION OF THE LARVA OF *BRACHYGASTRA SCUTELLARIS* (HYMENOPTERA: VESPIDAE)

By James M. Carpenter* and Kenneth G. Ross**

Introduction

Knowledge of the social structure in colonies of tropical Polistinae remains fragmentary. Since the pioneering studies of Richards and Richards (1951), capture and dissection of the adult population of a nest has been the primary method for reconstruction of the caste composition of a species. As the reviews of Jeanne (1980) and Akre (1982) document, long-term observational studies are increasingly contributing to behavioral analysis in this group. Yet the prevailing view of social structure in swarm-founding Polistinae is still largely based upon limited studies of a few species. Indeed, most of the species studied by Richards and Richards (1951) have not been re-examined.

While participating in the Second Cornell Suriname Expedition, the senior author collected five colonies of three of the species studied by Richards and Richards (1951), and one species studied by Richards (1978). Dissection of the specimens revealed certain discrepancies with the published accounts of colony composition for these species, as well as new information. These results are presented below, together with descriptive notes on the nests. The larvae of *Polybia bistriata, P. catillifex* and *Metapolybia cingulata* have been described by Reid (1942). He also described the larva of a *Brachygastra* species, termed by him *Nectarinia scutellaris.* However, Richards (1978: 166) stated that the nests he had obtained in Guyana, upon which Reid based his work, were actually those of the species *myersi.* The larva of *B. scutellaris* has thus never been described. A description is included in this paper.

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Methods

The colonies were collected during February 1982 in the Raleigh Vallen–Voltzberg Natuureservaat (Foengoe Eiland 4°42′N, 56°12″W, approximately 90 m elev.; Voltzberg Camp 4°42′N, 56°13′W, also 90m), Saramacca Dist., Suriname. The nests were placed in plastic bags and the adults killed with "wasp freeze". Adults and larvae were both preserved in Dietrich's fluid until dissection. All female wasps were dissected and various measurement data taken with an optical micrometer. Length of the discal cell (M1) was used as a measure of wing length; the left wing was excised and flattened in a drop of glycerin for measurement. No notable wing wear was found for any of the wasps. A modified Cumber ovariole index (Cumber, 1949) was used to quantify ovarian development, with an additional count of oocytes greater than 0.6 mm in length (considered "developed") as a check. Inseminated individuals could readily be distinguished by the pronounced reddish-golden color of the spermatheca; nevertheless all spermathecae were examined under phase-contrast microscope. Sperm were visible as an agglutinated mass in the lumen (Fig. 1). Classification into castes separated queens (inseminated individuals), intermediates (uninseminated but with an ovariole index of 1 or more) and workers (uninseminated, index = 0). Richards' gland (on metasomal sternum V) was present in all species (Fig. 2). No caste differences were observed in this structure.

Exploratory data analysis (Velleman and Hoaglin, 1981) was performed, with further analysis where results indicated. Analyses included investigations of the relationship between the various morphometric measures (were the correlations positive, and so reflections of general size?), the relationship between these and ovarian development (is size associated with reproductive capacity?), and differences between castes in these measurements. The data were normally distributed, therefore the results of t-tests are reported for caste differences.

Larvae were examined with the aid of cuticular stains (acid fuchsin, Grenacher's alcoholic borax-carmine, eosin-Y). Mouthparts and the frontoclypeal region of *B. scutellaris* were excised, and the latter examined under phase-contrast miscroscope.

Voucher specimens of all species have been deposited in the Cornell University Insect Collection, Lot number 1129.

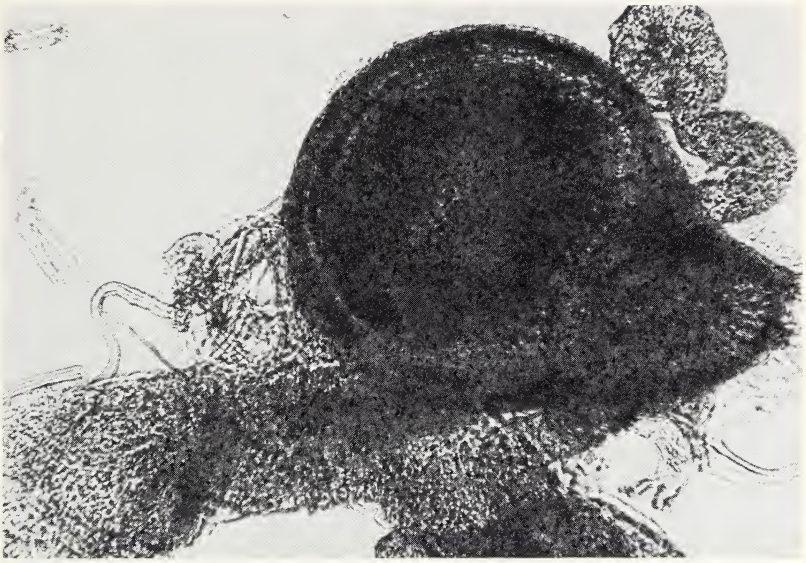


Fig. 1. *Brachygastra scutellaris*, spermatheca with sperm in lumen.

Results

Polybia bistriata:

Two colonies of this species were collected on Foengoe Eiland on February 4. The nests were located within 4 m of one another on the undersides of leaves in shaded secondary growth along a path. Both were about 1.5 m above the ground and thus inconspicuous. Several adults escaped from each nest.

The nests were similar in appearance, and of the same shape and size as depicted in Figs. 19–21 of Richards and Richards (1951). The envelope was whitish-gray with brown streaks, and moderately flexible. Under high magnification, fragments of plant tissue were distinguishable among masticated, somewhat granular material. The envelopes were built by the "edge technique" (Jeanne, 1973), and were not thickened. They were evidently the products of single construction efforts, and no growth lines were present. The entrances were slightly off-center and ventral, unlike Fig. 19 of Richards and Richards but like those described in the text (p. 56).

Fig. 2. *Polybia catillifex*, Richard's gland (700×), ventral view.

The first colony (82–02–04–1) contained a single comb of 147 uncapped cells, 24 of which contained early-instar larvae and 48 with eggs. These were concentrated in the center of the comb. No sign of cell re-use was present; the nest appeared to be quite young. Twenty-six adults were captured, six of which proved to be queens. Among the 20 workers, one had developing oocytes in the ovarioles, but these were still smaller than the accompanying trophocyte masses. Measurements consisted of maximum apical width of metasomal tergum I and length of this segment taken from the ligament base to the apex, as well as length of the discal cell. The tergal measurements were not significantly correlated with each other (all N=26; $r = .303$, Pearson product-moment correlation), but were correlated with length of the discal cell ($r = .482$, $p < .05$ for tergal width; $r = .488$, $p < .01$ for length). Hamulus number was not significantly correlated with any measurement ($r = .063$ for tergal width, .076 for length, and .157 for discal cell length). Only discal cell length was significantly correlated, negatively, with ovariole index

($r = -.443$, $p < .05$), however, the trends were also negative for the other measurements ($r = -.307$ for tergal width, $-.338$ for length, and $-.050$ for hamulus number). Queens did not differ significantly from workers in tergal width, discal cell length or hamulus number ($t = -1.883$, -1.917, and 0.070, respectively). Queens had significantly shorter terga than workers when compared by a t-test (mean = 1.47 mm versus 1.52, $t = -2.470$, $p < .03$).

The second colony (82-02-04-2) had a comb of 151 cells. Of these, 25 were capped, and some contained partly melanized pupae. There were also late-instar larvae in some uncapped cells; the number could not be ascertained due to damage to the nest, but was not greater than 12. Other cells were empty. No sign of cell re-use was present, and the occupied cells were irregularly arranged but mostly central. This colony was probably also producing its first brood. Forty-six adult wasps were taken, of which seven were queens and 39 workers. Of the latter, 11 had slightly developed oocytes, but the index was 0. The tergal width and length were significantly correlated, both with each other (all $N = 46$; $r = .375$, $p < .01$) and with length of the discal cell ($r = .567$, $p < .01$ for tergal width; $r = .726$, $p < .01$ for length). As in the previous colony, hamulus number was not significantly correlated with the other measurements. No measurements were correlated with ovariole index ($r = .026$ for tergal width, $-.032$ for tergal length, $-.219$ for discal cell, and $-.234$ for hamulus number). Queens did not differ significantly from workers by any measure ($t = 0.277$ for tergal width, -0.168 for tergal length, -1.495 for discal cell length, and -1.356 for hamulus number).

When the morphometric data for each colony were pooled, significant correlations were found between all measurements, but not hamulus number. When further examined, the colonies differed significantly in tergal width, with colony 2 having workers with narrower terga (mean = 0.73 mm versus 0.76; $t = -3.353$, $p < .002$). No correlation with ovariole index occurred in the pooled data, but all trends were negative. Summing up, it appears that queens are slightly smaller than workers but the differences are not generally significant in these young colonies.

Richards and Richards (1951) reported significant differences between queens and workers in hamulus number in this species, and this result has been widely cited (e.g. Richards, 1978; Jeanne, 1980).

They studied 14 colonies in varying states of development, and counted hamulus number in 138 wasps drawn from an unspecified number of these colonies. Queens had a larger average number of hamuli. While their results were based on a larger sample size, these authors could not check for sperm in the spermatheca, and so classified caste solely on the basis of ovariole condition. Workers were those with filamentous ovarioles and no "developed rudiments" (this term was not defined), and queens "nearly always" had some "ripe" eggs and a number of enlarged rudiments. They recognized an intermediate caste in three colonies, with "two or three rudiments more or less enlarged". These probably corresponded to our workers with some developed eggs (length $>$ 0.6 mm, index = 0). They further pointed out that their queens of one colony would have been classified as intermediates if "a typical queen" had been found. Without details on the source of their sample it is difficult to infer a complete explanation of their different results. However, their measure of wing length showed the same trend as ours: queens appear to be slightly smaller. The difference in mean hamulus number, with the queens having the larger value, may be at odds with this trend (cf. Richards, 1949 on a generally positive relationship between wing length and hamulus number). Therefore, some individuals were probably misclassified. At the very least, their result does not obtain for all colonies of this species (and probably not for all of theirs), and we believe it is generally not valid.

Polybia catillifex:

One colony of this species (82–02–03–1) was collected at Voltzberg Camp on February 2. It was in primary "liana forest" on a low vine, and inconspicuous. The envelope obscured the petiole, which was attached to a twig at the base of two leaflets. These had been curled around and attached to the apices of the peripheral cells, and the envelope also was built over their bases. The total area of the comb was approximately 38 x 32 mm. The paper was brown, and composed of tough plant fragments and some granular material. It was somewhat brittle, and had been built by the edge technique. Material had been added dorsally but in an irregular fashion; the envelope was considerably thicker dorsally. None of the projections figured by Möbius (1856: pl. 8, fig. 4) and described by Richards and Richards (1951: p. 64) were present. The envelope was incomplete ventrally, and the single comb exposed. There were approxi-

mately 95 cells. Eggs were present in nearly all of these, attached to sides of the cells just above the base.

The adults taken numbered 48, and three wasps escaped. Of the captured wasps, five were queens and 42 workers. One wasp was classified as intermediate, with an ovariole index of 1 but no developed eggs. It was our impression that its oocytes were degenerate, and we included it with the workers in the statistical analyses. Morphometric measurements included maximum width of metasomal tergum II as well as length of the discal cell. These were found to be significantly correlated with each other (all $N = 48$, $r = .410$, $p < .01$), and with ovariole index ($r = .375$ for tergal width and .499 for discal cell length, all $p < .01$). Hamulus number was not correlated with the morphometric measures ($r = .072$ for tergal width and $-.082$ for discal cell length) or ovariole index ($r = .198$). The queens were found to be significantly larger than the workers in both tergal width (mean = 2.49 mm versus 2.40; $t = 4.350$, $p < .002$) and discal cell length (mean = 4.91 mm versus 4.66; $t = 4.322$, $p < .004$). They did not differ in hamulus number ($t = -1.662$).

Richards and Richards (1951) studied four colonies of this species. They compared eight queens and eight workers (presumably determined solely by ovarian development) for five morphometric characters, and found no differences. Width of tergum II was not among these characters. They compared average wing length and hamulus number for ten queens and 33 workers, and found no differences. Their sample sizes were smaller than ours, and drawn from colonies in several stages of development (e.g. two colonies had two combs, and one of these had males). The fact that our colony had a larger number of workers than any of the colonies they studied, but a brood consisting entirely of eggs, suggests that this colony was the recent product of a swarm. This is supported by the incomplete envelope of our colony. Therefore the larger size of queens found by us may be characteristic of recently initiated colonies of this species, and not necessarily mature colonies.

Brachygastra scutellaris:

One colony of this species (82-02-11-1) was collected at Voltzberg Camp on February 11. It was on a branch tip of small *Clusia* tree on the granite outcrop near the camp. The nest was about 1.65 m high and readily visible. In general appearance it was of much the same form as Figs. 7 and 8 of Richards and Richards (1951). The

envelope was brownish-gray and quite flexible. The paper consisted of fine whitish fibers and plant epidermal fragments. Some thickening of the envelope had occurred, but was not uniform. The envelope for each comb appeared to be the result of a single construction effort, and was attached to the edge of the combs. The entrance was at the edge of the ventral surface, and more or less continuous with the entrances to each comb.

There were three combs. The oldest, basal comb contained 113 cells, of which 48 were capped and contained pupae. These were concentrated in the center of the comb. Many of the pupae were melanized, and three adults were emerging as the nest was collected. The cells around the periphery of the capped cells contained 11 late-instar larvae. The second comb consisted of 163 cells, of which 118 were capped and contained pupae and prepupae. In addition, 16 uncapped cells contained late-instar larvae. The third comb had 232 cells. There were 18 early-instar larvae scattered about the comb, and an indeterminate number of eggs at the bottom of many cells (the edges of the comb were crushed, but the cells did not appear to have eggs).

The number of adults taken was 112; 2 escaped. Among the captured wasps were 23 teneral individuals classified as "callow". These were measured and dissected, but omitted from most of the statistical analyses (all had filamentous ovarioles). The remainder consisted of 34 queens, 22 intermediates and 33 workers. Measurements included maximum width of metasomal tergum II in addition to length of the discal cell. Following Richards and Richards (1951) for the species *myersi,* the number of individuals with reddening of the proximal part of the metasoma, and the degree of yellow coloring of the scutellum were recorded.

Tergal width and discal cell length were significantly correlated (all $N = 112$, $r = .271$, $p < .01$). Neither measure was correlated with hamulus number ($r = -.046$ for tergal width, .214 for discal cell length), although the alpha level was close to .05 for discal cell length. Discal cell length was significantly correlated with ovariole index ($r = .309$, $p < .01$), but tergal width ($r = .080$) and hamulus number ($r = .171$) were not. No significant association of measurements with color pattern were found. When the three castes were compared by ANOVA, width of tergum II was not different ($F = 1.08$, $df = 88$). Length of the discal cell was significantly differ-

ent, with queens having longer wings (mean = 2.71 mm versus 2.57 for intermediates and 2.62 for workers, $F = 24.54$, $df = 88$, $p < .005$). Hamulus number was not different ($F = 2.39$, $df = 111$; callows included), but when intermediates were lumped with workers queens were found to have a significantly higher average value (mean = 7.5 versus 7.2; $t = 2.604$, $p < .02$). When reddening of the metasoma was tested by a chi-square for differences among castes, workers were found to have a greater degree of reddening than expected, and queens were darker than expected (none had any reddening), with intermediates falling between ($X^2 = 13.31$, $df = 2$, $p < .005$). Scutellar color could not be tested in this way, as almost all specimens were classified as "entirely yellow"; obviously there were no differences between castes.

Richards (1978) reported on two colonies of *B. scutellaris*. He dissected 173 individuals, evidently preserved in alcohol, and compared 30 queens with 30 workers (drawn equally from the two nests) for forewing length, number of hamuli, number of hamuli per mm of wing length and width of tergum II. Color pattern was also compared, but he did not give details. Richards did not find differences in most of these features, but detected a significant difference in hamulus number, with queens having a smaller mean number (7.07 versus 7.53). This result is directly contrary to ours, but again, there are problems with his classification into castes. He evidently separated intermediates from queens on the basis of size of the eggs ("partly developed" versus "large"), but stated that this division was "not sharp" in the first colony and termed the egg counts "rather arbitrary" in the second colony. He did not record any intermediates for the second colony but stated that some of the queens "might have been called intermediates". It is therefore likely that some individuals were misclassified. Our sample size was larger than his, and his result of a significantly lower mean hamulus number but a slightly larger size for queens than workers (differences not significant) is contrary to the presumed general relationship (Richards, 1949), as well as to the results of our study. It is possible that the relationship varies between colonies, but there is probably a general tendency for queens to be larger in this species. Color pattern is apparently largely independent of reproductive status. Scutellar color was not associated with caste or ovariole development in our colony, and Richards and Richards (1951) found opposite tenden-

cies in the two colonies of the closely related species *B. myersi*. Their results for metasomal reddening for one nest were similar to ours (association of this and caste were not reported for the other colony), with reddening occurring only in workers among their dissected wasps. The basis of this association is unknown, but it certainly does not arise from any "effect of dissection" as the Richardses speculated, for we recorded color before dissection.

Metapolybia cingulata:

One colony of this species (82–02–08–a) was collected on February 8 at Voltzberg Camp. It was oriented obliquely on a large granite boulder in "mountain savannah" forest, and was about 0.5 m above the ground and well shaded. The envelope was of the same color as the lichen- and moss-grown rock face, and so the nest was very well camouflaged. It measured 6.35 by 4.45 cm in surface area, and the entrance was on the upper surface towards the lower end. The paper was green-gray, very flexible and composed of crumbly fragments in a matrix of secretion. It was uniformly thin. The secretion formed the "windows" (Richards and Richards, 1951) scattered throughout the envelope. The paper forming the comb was brown and composed entirely of granular material overlain by secretion. The cells were separated from the envelope, and there were a minimum of 222 (some were destroyed during removal). No brood was found.

Adults collected numbered 38, and approximately ten escaped. There were two queens, 33 workers and three males. Among the workers, four had an ovariole index ranging from 1 to 4 but none of these had any "developed" eggs (length greater than 0.6 mm). They were therefore treated as workers in the analyses. Measurements included maximum width of tergum II and length of discal cell. These were significantly correlated with each other (all $n = 35$, $r = .586$, $p < .001$), but not with hamulus number ($r = .208$ for tergal width, .188 for discal cell length). None of these measures was correlated with ovariole index ($r = .179$ for tergal width, .115 for discal cell length and .182 for hamulus number). Queens were not different from workers in tergal width ($t = .699$) or hamulus number ($t = 1.2216$). In length of the discal cell, the castes differed significantly by a t-test (mean = 2.74 mm for queens versus 2.82 for workers, $t = -4.776$, $p < .001$), but not by a Mann-Whitney test ($T = 14$). The former test has more power, but in view of the small

number of queens it is probably best not to attach great importance to the result. In a previous study of this species (Richards and Richards, 1951) no external indication of caste was found, and our findings are in line with this.

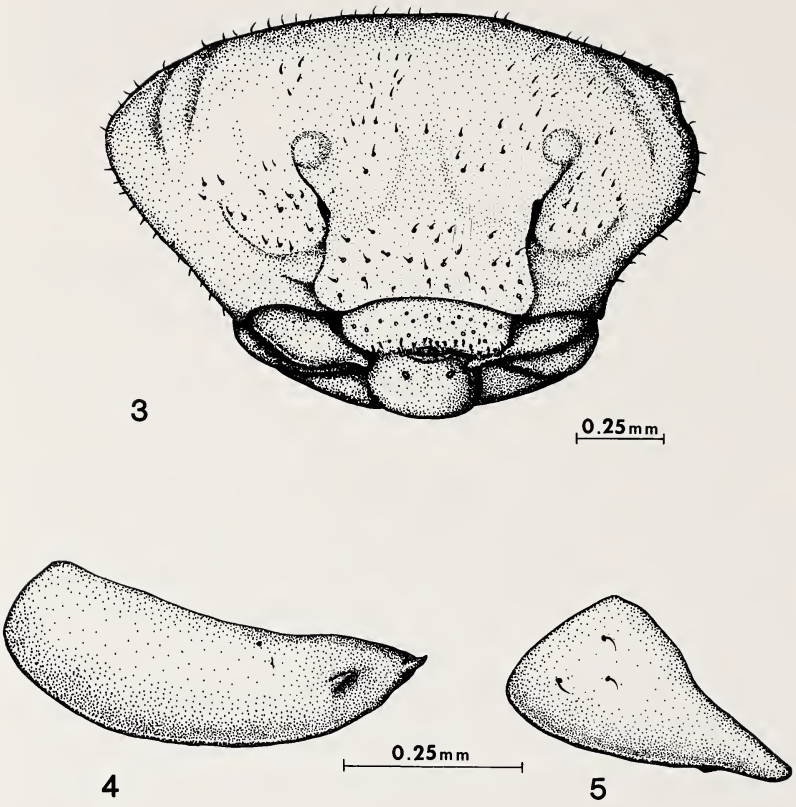
The Larva of *Brachygastra scutellaris*

As noted previously, Reid's (1942) description was actually of the species *myersi*. A series of larvae from a second colony of *B. scutellaris* was present in material from the British Museum (Natural History) examined by the senior author; the label data are: Brazil: MT, base Camp, dry forest/22.IX.68.N. 152. OWR". The following description is based upon both colonies. All measurements are of late-instar individuals.

Length 5.7–7.8 mm; maximum width 2.2–3.5 mm. Head and body pale. Dorsal lobes (paired ridges) present on first 4 abdominal segments. Pleural lobes strongly developed; no division into annulets. Integument essentially smooth. All spiracular openings subequal in size, more or less circular. Anus with ventral lips forming a bilobed slit.

Head width 1.6–1.8 mm; height (exclusive of labrum) 0.6– 0.8 mm. Head capsule very soft. Setae scattered over surface, varying in number (fig. 3). Ecdysial line and parietal bands weakly indicated, the latter smooth. Anterior tentorial pits below antennal orbits. Clypeus of the usual polistine form; frontoclypeal sulcus effaced dorsally. Labrum approximately as wide as interantennal distance, sinuate; surface roughened ventrally, with 8–10 or more papillae. Mandible as in fig. 5; 2 or 3 setae on external surface. Maxilla as in fig. 4; bases further apart than mandibular bases. Labium setate; salivary opening a raised transverse slit behind palpi.

In addition to *scutellaris,* specimens of *B. augusti, bilineolata, moebiana* and *lecheguana* from the collection of the British Museum have been examined. The more transverse shape of the head in fig. 3 than the species figured in Reid (1942) and Dias Filho (1975) is perhaps a preservational artifact, related to the softness of the head capsule. However, it was present, with some variation, in all specimens seen. The genus is also uniform in the setae of the head capsule and the mandible with a weak ventral tooth, both diagnostic characters in Richards (1978). Presence of setae on the mandibles is



Figs. 3–5. Larva of *Brachygastra scutellaris:* 3, frontal view of head capsule; 4, mandible; 5, maxilla.

another major character in Richards' key to genera (with the exception of *lecheguana*), but care must be used in this feature. Number of setae varied within the 2 colonies, but was always low.

Conclusion

Our results support the general view that caste dimorphism is poorly developed or absent among Polistinae. Where differences were found *(Polybia catillifex, Brachygastra scutellaris),* queens were larger than workers. Among the Polistinae where differences have been detected, queens are the larger caste, except in a few

swarm-founding species (Jeanne, 1980). Such morphological differences between reproductives and non-reproductives may vary between colonies of the same species (Richards and Richards, 1951; Jeanne and Fagen, 1974; this paper) and within colonies over the course of a normal cycle. Moreover, although morphological caste differentiation is not pronounced in the Polistinae, behavioral and functional differentiation is well developed (West Eberhard, 1978).

Lack of pronounced morphological caste dimorphism has been taken to indicate a less advanced level of eusociality in the Polistinae relative to the Vespinae (e. g. Iwata, 1976). However, by other criteria of social complexity (mode of suppression of nestmate reproduction, colony size, duration of colonies), the swarm-founding Polistinae are at a comparable level of sociality to the Vespinae (Jeanne, 1980). The difference in degree of caste dimorphism between the two groups of highly social wasps undoubtably reflects ecological constraints of the environments in which they have evolved (Richards, 1971), with the strong queen/worker dimorphism of the Vespinae part of an adaptive syndrome linked with winter hibernation and a short colony life cycle (Richards, 1971). The differences in adult size between queens and workers of some polistine species suggest that in these species caste differentiation is either pre-imaginal, or that males preferentially mate with females possessing certain morphological attributes (or that only these females are receptive to mating). These competing hypotheses must be tested in species in which caste dimorphism has been firmly established.

Although dissection and morphometric study of individuals collected with nests are likely to remain the primary methods of analysis of social structure in tropical polistines, the information provided is limited. A proper understanding of the social biology of these wasps requires in-depth behavioral studies of natural colonies.

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THE PERSISTENCE OF ROLE IN EXTERIOR WORKERS OF THE HARVESTER ANT, *POGONOMYRMEX BADIUS*

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The social organization of an ant colony channels individuals into particular tasks, so that the colony continues to perform its tasks in a regular way. In other words, the colony is organized so that certain roles (*sensu* Oster and Wilson 1978), vital to its function, continue to be filled. The present study reports on role behavior in exterior workers of the harvester ant *Pogonomyrmex badius.*

Three questions are addressed: 1) In *P. badius,* do particular groups of ants consistently do certain tasks? 2) Does the task performed by an ant depend on its age? Because *P. badius* workers live for about a year (Porter and Tschinkel 1982), marked individuals were observed for a longer time (up to four months) in the present study than in previous studies of *Pogonomyrmex* species (Hölldobler 1976, Porter and Jorgensen 1981). 3) Does the task performed by an ant depend on its size? *P. badius* is the only polymorphic species in its genus. Since majors rarely emerged from the nest, only the role behavior of minor workers was considered in this study. However, even within the minor subcaste of *P. badius,* a greater size variation exists than in other *Pogonomyrmex* species. The relationship between size and role in *P. badius* minors is investigated.

In the present study, the behavior of exterior workers is classified into a more detailed set of tasks than in previous studies of the genus. Foraging, i.e. food retrieval, is only one of five activities observed outside the nest. The classification of tasks used here is needed to explain other aspects of *Pogonomyrmex* behavior (Gordon 1983a and b).

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Methods

All experiments were conducted in the laboratory with five queen-right colonies of *P. badius,* each containing about 650 workers. The presence of brood inside the nest could not be ascertained. Colonies were kept in soil-filled tanks (45 × 25 × 20 cm), and fed with Bhaktar-Whitcomb diet (1970), which was placed on the soil surface in a small dish. Individual ants were marked with Testors Gloss Enamel, each with a drop on the top of the head. Single ants were kept isolated overnight after being marked, and then put back into the home colony. No adverse reactions to the marking procedure were observed.

All tasks performed by ants outside the nest were classified into the following five activities (Table 1): Foraging, Nest Maintenance, Patrolling, Midden Work, and Convening. Ants inside the nest were not considered in this study. No majors were marked, since they spent almost all of their time inside the nest, probably assisting in brood care (pers. obs.).

An observation record consisted of the numbers of marked and unmarked ants in each of the five categories of behavior. Observations were made between 8:00 and 20:00. Each observation lasted 5–10 minutes, depending on the total number of ants outside the nest. At least one hour elapsed between successive observations.

A. *Continuity of role.* In each of the five colonies, ants collected while performing one of the five categories of behavior were removed from the colony and marked. For example, in one colony only foragers were marked, in another only patrollers were marked, and so on. In each colony, five ants were marked every five days until 20 ants had been marked. Each group of five ants was marked with paint of a different color. Thus each colony was observed for a total of 35 days, which I call the first observation period. During this time, a total of 728 observations were made, about 145 observations on each colony.

The data were analysed separately for each colony as follows. First, a two-way chi-squared procedure with four degrees of freedom (Sokal and Rohlf 1981) was used to test whether the distribution of the ratio of marked to unmarked ants depends on activity. Next, another chi-squared test, this time a two-by-two test with one degree of freedom, was performed. The latter tested whether ants were significantly likely to continue doing the activity they were doing when marked, called the "tagged activity." Both tests used the total

Table 1. Classification of activities of exterior workers of *P. basius* in laboratory colonies

Foraging	A. Standing at the food dish, eating.
	B. Taking food items into nest.
	C. Piling sand on food.
Nest Maintenance	A. Carrying sand out of nest, putting it down and going back into nest.
	B. Rearranging sand on terrarium surface.
Patrolling	A. Walking around edge of terrarium, inspecting sides with antennae.
	B. Walking around with abdomen tucked under thorax, with frequent stops and changes of direction.
	C. Pawing at sand with front legs and inspecting the resulting small depression with antennae.
Midden Work	A. Repiling midden.
	B. Standing on midden.
	C. Carrying objects (dead ants, food bits, twigs, etc.) to midden.
Convening	A. Standing with a group, grooming each other.
	B. Standing with a group, self-grooming.
	C. With a group milling around slowly under the lamp, sometimes inspecting others of the group with antennae.

numbers of marked and unmarked ants observed in each activity, during the entire observation period. The latter, two-by-two test used the total numbers of marked and unmarked ants observed in the tagged activity, and the two summed values for the other four activities.

B. *Death rates of marked ants.* To determine whether death rate differed according to activity, the colony middens were inspected daily during the first observation period, and dead marked ants were counted.

C. *Continuity of role after a two-month interval.* The observations described in part A were ended on July 12, 1982. On September 12, 1982, observations of the same marked individuals in the same five colonies were begun again and continued for 25 days, which I call the second observation period. A total of 193 observations were made, and the data were analysed as before.

D. *Behavior of callow workers.* Adult ants that have recently emerged from the pupal stage, or callows, are lighter in pigment than older adults. Their behavior was examined in two ways. First, for 25 days during the second observation period, the number of callows in each of the five activities was recorded, as well as the numbers of all other ants. Records were obtained on only two colonies, since the other three colonies had but few callows outside the nest. These data, consisting of 81 observation records, were analysed as in Part A with a two-way chi-squared procedure. This tested whether the distribution of the observed number of callows depended significantly on activity.

Second, 20 convening callows in one colony were marked, using the procedure described in part A. They were observed for 40 days, beginning with the day on which the first group of five callows was marked. Convening callows were chosen because it was rare for a callow to be seen doing any of the other four activities. A total of 149 observations were made in this procedure. The data were analysed as in parts A and C.

E. *Relation of body size to activity.* To determine whether body size is correlated with activity, the head widths of 25 minors in each of 7 colonies, a total of 175 ants, were measured. Each group of 25 ants consisted of 5 ants from each of the five categories of behavior, or activities. Head width was measured at right angles to the line between the clypeus and occiput, immediately posterior to the eyes,

using an ocular micrometer calibrated in 0.1 mm. Measurements were estimated to the nearest 0.01 mm. The data were subjected to a two-way analysis of variance (Sokal and Rohlf 1981), which tested for the effect of activity and colony of origin on head width and for a colony-activity interaction.

Results

A–C. *Continuity of role.* In both observation periods, the ratio of marked to unmarked ants depended highly significantly on activity in all five colonies (two-way chi-squared test, $p < 0.0001$ for all tests). Table 2A shows the data from the first, 35-day observation period (part A). The deviations shown are based on the expected values derived in the two-way test for each colony. The significance values along the diagonal of the table are the result of the two-by-two chi-squared tests of whether marked ants continued to do the tagged activity. These results all show highly significant, positive deviations from the expected values. All groups of ants continued doing the activities that they were doing when marked. Thus, the data of Table 2A show that groups of ants do specialize in certain activities.

Cells not on the diagonal in Table 2A show the data for ants in the four activities other than the tagged one. In some cases, the data show a large positive deviation from the expected value in an activity other than the tagged one. This indicates that marked ants were likely to perform a second activity as well as the tagged one. The results shown in Table 2A, and summarized in Table 2C, lead to the following conclusions.

Ants marked while doing midden work tended to be later engaged in patrolling, and vice versa, indicating that midden work and patrolling are done by the same ants. Ants marked while convening later did midden work as well. But ants marked doing midden work did not later do convening. Similarly, ants marked while doing nest maintenance later did patrolling as well. But ants marked while patrolling did not later do nest maintenance. These results suggest that ants marked while convening were in transition to midden work, and that ants marked while doing nest maintenance were in transition to patrolling. In these two colonies, I examined the proportions of marked ants doing each activity as a function of time in the course of the first observation period, but saw no interesting or possibly significant changes in these proportions. The possibility of later role

changes of ants marked while convening or doing nest maintenance is discussed below.

The numbers (each out of 20) of dead marked ants in the first observation period were as follows: midden workers, 11; patrollers, 16; foragers, 2; conveners, 1; nest maintenance workers, 2.

Table 2B shows the data from the second, 25-day observation period, begun two months later. Several obvious differences between the data of Table 2A and that of Table 2B should be noted. Fewer observations (149) were made in the second observation period than in the first one (728). The colony in which patrollers were marked was barely active during the second observation period, for unknown reasons. Colony inactivity was not accompanied by any obvious increase in the number of dead workers visible in the midden. Because no marked ants were observed, it was not possible to analyse the data from this colony. As noted above, many midden workers and patrollers died during the first observation period. Though only two marked foragers died during this first 35-day period, the number of marked foragers had decreased two months later, indicating that many foragers died during the interval between the first and second observation periods.

The two-by-two tests for the second observation period show that marked ants were no longer likely to do the tagged activity. All marked ants had either died or changed activity after a two-month

Table 2(A–D). Behavior of marked ants
(Pages 000–000)

In Tables 2A and 2B, each row of the matrix shows the results from one colony, in which ants were marked doing the indicated activity. The first five columns show the subsequent activities of marked ants. In each cell are shown the total numbers of marked and unmarked ants observed during the entire observation period, the deviation from the expected value, and the percent deviation (of the expected value). **means $p < 0.001$; NS means "not significant." The last column shows the mean number of marked ants per observation.

Table 2C summarizes Tables 2A and 2B. It shows the results of the two-by-two chi-squared tests of whether marked ants continue doing the tagged activity. Also shown are strong positive deviations from expected values in other activities. Plus and minus signs indicate the sign of the deviations from expected values. As in Tables 2A and 2B, each row of the matrix shows the results from one colony, in which ants were marked doing the indicated activity.

Table 2D is similar to Tables 2A and 2B. It shows the data from part D, in which callow ants were marked when convening.

Table 2A. Behavior of marked ants during first observation period.

Activity When Marked		*Subsequent Activity* F	NM	PT	MW	CN	Mean no. marked ants seen per observation
F		**					
	Marked	47	126	26	16	29	2.28
	Unmarked	309	1397	281	373	568	
	Dev. for Exp.	+19.6	+8.8	+2.4	−13.9	−16.9	
	% Dev.	.72	8	10	46	36	
NM			**				
	Marked	37	436	116	134	184	5.60
	Unmarked	623	4755	1112	2764	2915	
	Dev. for Exp.	−8.8	+75.9	+30.8	−67.0	−31.0	
	% Dev.	19	21	36	33	14	
PT				**			
	Marked	23	34	123	173	48	2.18
	Unmarked	397	2776	904	1736	1309	
	Dev. for Exp.	+0.6	−115.8	+68.3	+71.2	−24.3	
	% Dev.	3	77	125	69	34	
MW					**		
	Marked	9	67	102	343	276	7.05
	Unmarked	242	1514	819	1840	4688	
	Dev. for Exp.	−11.2	−60.3	+27.9	+167.3	−123.6	
	% Dev.	55	47	38	95	30	
CN						**	
	Marked	50	325	131	245	313	6.57
	Unmarked	404	2481	701	1124	1362	
	Dev. for Exp.	−17.7	−93.4	+6.9	+40.9	+63.3	
	% Dev.	26	22	6	20	25	

F = Foraging; NM = Nest Maintenance; PT = Patrolling; MW = Midden Work; CN = Convening.

Table 2B. Behavior of marked ants during second observation period

		NS					
	Marked	11	3	29	32	91	
F	Unmarked	130	458	566	557	721	0.64
	Dev. for Exp.	+2.0	−26.5	−9.0	−5.6	+39.1	
	% Dev.	22	89	24	15	75	
			**				
	Marked	11	8	133	41	5	
NM	Unmarked	264	925	1289	994	937	3.94
	Dev. for Exp.	−0.8	−32.1	+71.9	−3.5	−35.5	
	% Dev.	7	80	118	8	88	
	Marked	0	0	0	0	0	
PT	Unmarked	7	12	13	15	0	0
	Dev. for Exp.	–	–	–	–	–	
	% Dev.	–	–	–	–	–	
					**		
	Marked	4	2	41	11	67	
MW	Unmarked	76	136	360	417	165	0.74
	Dev. for Exp.	−3.8	−11.5	+1.8	−30.8	+44.3	
	% Dev.	48	85	5	74	195	
						NS	
	Marked	23	4	46	40	12	
CN	Unmarked	128	375	488	529	192	2.23
	Dev. for Exp.	+12.7	−21.8	+9.7	+1.3	−1.9	
	% Dev.	55	84	26	3	14	

F = Foraging; NM = Nest Maintenance; PT = Patrolling; MW = Midden Work; CN = Convening.

Table 2C. Summary of results from first and second observation periods

	First Observation Period				
Activity when Marked	*Subsequent Activity* F	NM	PT	MW	CN
F	** +				
NM		** +			+
PT			** +	+	
MW			+	** +	
CN				+	** +

	Second Observation Period				
Activity when Marked	*Subsequent Activity* F	NM	PT	MW	CN
F	NS				+
NM		** −	+		
PT					
MW				** −	+
CN	+		+		NS

F = Foraging; NM = Nest Maintenance; PT = Patrolling; MW = Midden Work; CN = Convening.

interval. Ants originally marked while convening now appeared to do foraging instead. Ants marked while doing midden work now did convening, as did those marked while foraging. Finally, ants marked while doing nest maintenance now tended to do patrolling. These results are summarized in Table 2C.

D. *Behavior of callow workers.* The two-way chi-squared test on the data on callow workers shows that the ratio of callows to other ants depends highly significantly on activity ($p < 0.0001$). In both colonies in which callows were observed, the callows were most often observed convening.

Callows that were marked while convening and observed for 35 days were significantly likely to continue to convene ($p < 0.0001$ for two-way chi-squared test, $p < 0.001$ for two-by-two chi-squared test) (Table 2D). Although dark-pigmented, older ants marked while convening were also likely to do midden work during the first 35 days (Table 2A), it appears that convening callows were *not* likely to do midden work (Table 2D).

The results of these two procedures show that callow ants convene for at least 35 days. Although in the field *P. badius* callows acquire darker, adult coloration within 25 days (Gentry 1974), only 6 of the 20 callows marked while convening were as dark as non-callow adults at the end of 40 days. The others were still of intermediate coloration.

E. *Body size.* There was no significant relationship between head width and type of activity in minor workers. The two-way anova showed no interaction between colony of origin and type of activity ($DF = 24$, $SS = 0.44$, $F = 0.64$, $p > 0.8993$), no effect of type of activity on head width ($DF = 4$, $SS = 0.09$, $F = 0.77$, $p > 0.5492$), and a significant effect of colony of origin on head width ($DF = 6$, $SS = 1.30$, $F = 7.53$, $p > 0.001$). Mean head size for all 25 workers in all five activities ranged from 1.53 mm in one colony to 1.78 mm in another of the seven colonies. Mean worker size increases with colony age (Oster and Wilson 1978). Differences in age among the seven colonies probably account for the effect of colony of origin on head width.

Discussion

At any one time, exterior workers in the *P. badius* colony can be divided into four groups that consistently perform certain roles for at least 35 days: 1) midden work and patrolling, 2) nest maintenance, 3) foraging, and 4) convening.

Table 2D. Behavior of callows while convening

	Activity when Marked	*Subsequent Activity* F	NM	PT	MW	CN
						**
CN	Marked	26	17	63	74	385
	Unmarked	2290	14382	4664	9731	15601
	Dev. for Exp.	−1.7	−155.2	−6.5	−43.3	+193.8
	% Dev.	6	90	12	37	101

F = Foraging; NM = Nest Maintenance; PT = Patrolling; MW = Midden Work; CN = Convening.

Convening of exterior workers is observed much more often in the laboratory than in the field. Convening includes resting and mutual grooming. It probably serves a thermoregulatory function as well, because convening ants in laboratory colonies always gather in the warmest place on the terrarium surface, directly underneath a lamp. Convening has been observed in field colonies of *Pogonomyrmex,* but only rarely (MacKay 1981; Gordon 1983b, 1984a, b). It is possible that, in the field, convening is usually done inside the nest where conveners would be less subject to predation.

The results of this study, summarized in Table 2C, suggest the diagram depicted in Figure 1. The diagram shows how role may depend on worker age in exterior workers of *P. badius.* It should be emphasized that the diagram is hypothetical, pending further investigation, and that it rests on two assumptions. In keeping with results on many other species (Wilson 1971), it is assumed that younger ants first work inside the nest, then work outside the nest for the remainder of their lives. Another assumption is that in the laboratory experiments reported on here, the death rate of ants in a particular activity depends on their age rather than on the hazards or energetic costs associated with their activity. Convening ants are clearly less active than ants in the other four activities (see Table 1). However, there is at present no empirical basis for distinguishing the other four activities in terms of the energy expended performing them.

Ants doing midden work and patrolling are shown as the oldest in Figure 1, because ants marked while doing these activities died within

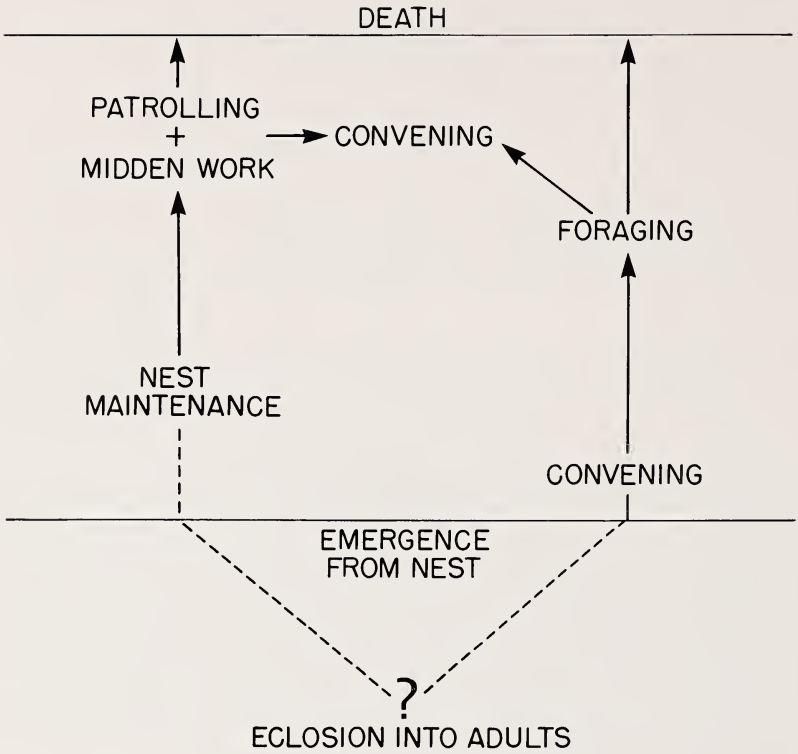

Fig. 1. How role depends on age in exterior workers of *P. badius*. The vertical direction represents worker age.

35 days, sooner than ants in any of the other groups. It seems that convening is done at two different times in the life of *P. badius* individuals. One group of conveners is the youngest group shown, because callows are most likely to convene, and continue to do so for at least 35 days. The results from the second observation period suggest that convening ants become foragers, and some foragers later become conveners, as shown. Since marked midden workers did convening in the second observation period, an arrow is drawn from the patrolling and midden work group to the older convening group. There is evidence that this transition may also be made in the opposite direction: some ants marked while convening (not callows —see Part A) did midden work in the first observation period, and patrolling in

the second. Marked nest maintenance workers were probably in transition to patrolling during the first observation period. Later, nest maintenance ants became patrollers, as shown.

The results of Porter and Jorgensen (1981) for *P. owyheei* suggest a schema similar to the one of Figure 1. Foraging, for these authors, may include midden work, patrolling, convening and foraging as they are defined in Table 3. By examining the behavior of foragers in more detail, the present study indicates the existence of at least one group of ants older than those engaged in food retrieval: ants doing both midden work and patrolling. The relationship between these two activities will be addressed in a subsequent paper (Gordon 1984b). It would be interesting to examine role behavior in field colonies of *P. badius* using the classification of behavior employed in the present study.

I do not attempt in this study to describe division of labor in the *P. badius* colony as a whole, because the behavior of interior workers is not considered. But the results raise several questions about age polyethism in exterior workers. First, there appear to be two groups of exterior workers in the colony. Ants of one group first do convening and then foraging, while ants of the other first do nest maintenance and then midden work and patrolling. It appears that ants from either group may then become conveners. What determines to which group an ant will belong? The possibility that these groups correspond to different sizes of workers within the minor subcaste was examined, but I found no such relationship. Second, exactly how long do individual ants remain in each of their roles? For a long-lived species like *P. badius,* the answer to this question awaits a marking technique better than the one used in this study. After about four months, some of my marked ants were seen to have most of the paint chipped off.

The unresolved questions in this study are part of a larger one: how is the distribution of workers into different roles regulated? There is considerable evidence that individuals are channelled into particular roles according to the current needs of the colony (e.g. Meudec and Lenoir 1982, Lenoir and Ataya 1983, Wilson 1983). To answer the questions raised by this study, we must come to understand the system by which the colony assesses and predicts what needs to be done.

Summary

Exterior workers in laboratory colonies of the southern harvester ant, *Pogonomyrmex badius,* were marked while performing one of the following: 1. midden work, 2. patrolling, 3. nest maintenance, 4. convening, or 5. foraging. These activities were consistently performed by marked ants for at least 35 days. The results indicate that the five activities are performed by four distinct groups of ants; it appears that midden work and patrolling are done by the same ants. Three months after marking, conveners had become foragers, and nest maintenance workers had become patrollers. Younger, callow ants were most often observed convening. Midden workers and patrollers died sooner than other marked ants. These results show how role may depend on worker age. In this species the minor caste is continuously polymorphic, but no evidence for size polyethism within the minor caste was found.

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PHENOLOGY AND LIFE HISTORY OF THE FILMY DOME SPIDER (ARANEAE: LINYPHIIDAE) IN TWO LOCAL MARYLAND POPULATIONS*

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Introduction

The filmy dome spider *Neriene radiata* (Walckenaer) [= *Linyphia* (*Prolinyphia*) *marginata* C. L. Koch; Araneae, Linyphiidae] spins a fine, dome-shaped web in the understory vegetation of temperate forests. Early accounts suggested that this species has a typical annual life cycle; however, later research uncovered indirect evidence of a mixed life-history pattern in a Michigan population of *N. radiata* (Wise 1976). Seasonal changes in composition of this population strongly suggested that some hatchlings emerging from egg sacs laid in the spring developed rapidly, matured by August and reproduced before the end of the season. Other progeny of spring-maturing adults apparently displayed a typical annual life cycle, over-wintering as juveniles and maturing the next spring. Since this type of life cycle had not been reported often for spiders, I decided to explore it in more depth.

The research reported here had two major goals:

1) To describe the phenologies of two different local populations of *N. radiata* in Maryland, and to compare them with the phenology of the more northern Michigan population. Such a comparison would indicate whether or not the length of the growing season might influence the species' life history pattern.

2) To obtain direct proof of two types of juveniles in the population at the end of the spring reproductive period—rapid developers, and those that over-winter before becoming mature. The goal was to confirm the previous interpretation of the observed phenology, which was based upon indirect, nonexperimentally derived evidence.

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Methods

The research, conducted at two sites 35 km apart, involved censusing undisturbed areas, manipulating the age structure of one population in a field experiment, and rearing field-collected juveniles from both populations.

Study Sites

The terrain of the oak forest on the Liberty Watershed, 40 km northwest of Baltimore, Maryland, was hilly, with rocky outcroppings, fallen trees and small saplings offering a variety of substrates for *N. radiata* to attach its web. A population at the Liberty site, on a south-facing slope at 180 m elevation, was studied 1980–82.

The Patuxent site was located south of Liberty on the Patuxent Wildlife Research Center near Laurel, Maryland, at an elevation of 40 m. The oak forest at Patuxent differed from that at Liberty by having several beech and some pines. The terrain was flatter, with no rocky outcroppings and with a floristically less diverse understory. Much of the Patuxent ground cover was *Vacunium* sp. Relatively rare at Patuxent before 1980, the filmy dome spider was more common 1981–82. During these years several studies were done with the Patuxent population.

Determining the Phenological Pattern in Maryland Populations

During 1980–82 I monitored seasonal changes in the size-class structure of the Liberty population by repeatedly censusing 13 areas marked with short, inconspicuous stakes. At Patuxent 8 similarly marked areas were censused, but in 1982 only. Mature *N. radiata* were collected at Liberty (spring, 1980–81; summer, 1980) and Patuxent (spring and summer, 1981–82) by capturing every adult encountered during a search of vegetation in the vicinity of the areas set aside for censusing. These spiders provided data on yearly and seasonal changes in size at maturity and fecundity. Collected adults were anesthetized briefly with CO_2, measured and then paired in jars kept in the laboratory (1980–81) or on a covered, screened porch in the forest at Patuxent (1982). The spiders were fed fruit flies *ad lib.* Females deposited an egg sac within one to several days after being collected. Each sac was removed, eggs were counted and the diameters of 10 eggs were measured with an ocular micrometer. In 1982 all the eggs from a sac were then placed in a 7 × 10 mm plastic vial and its open end was plugged with silk from the egg sac. The vial was placed in a humid jar, where the eggs were left

to develop. Many females continued to feed and deposited additional sacs. However, because the frequency of multiple clutches in nature is unknown, data are given for the first sac only.

Temperatures of web sites were recorded concurrently at Patuxent and Liberty with thermocouple probes on 24 May and 8 June, 1983. Each probe was covered with black tape, so that its temperature closely approximated the internal temperature of a filmy dome spider exposed to solar radiation (personal obs.). Sites selected for recording temperature originally had a *N. radiata* web and, as a group, spanned the range of exposure to wind and sunlight of webs at each study site.

Direct Evidence for Different Rates of Development

Field Experiment

During the last half of the season, *N. radiata* populations characteristically contain all stages. This diversity makes it difficult to follow the growth and development of groups of juveniles. Therefore, a manipulative field experiment was designed to facilitate monitoring of the developmental pattern of the younger spiders in the population.

Eight experimental units were placed at least 10 m apart in the undergrowth at Patuxent. Made of wood stakes that supported undulating pieces of 5.1 cm-mesh galvanized wire fencing (chicken wire), each unit was 3 m long, 1 m wide and 1 m high. Use of these standardized units made it possible to establish open, replicated populations of similar densities and microclimatic conditions, and also facilitated identification of the experimental populations.

From 8–17 July 1981, filmy dome spiders were removed from the units and from surrounding vegetation. The smaller instars, all of which had emerged from egg sacs laid by spring-maturing females, were then added at random to the cleared units. On 21 July (Day 0 of the experiment) each unit contained 20–39 spiders ($\bar{x} = 30 \pm 2$), all estimated to be stages 2–4. This range represented the youngest instars in the Patuxent population on that date.

Four randomly selected populations received supplemental prey from 21 July through 28 August. On 21 days each spider was given a living fruit fly; on 5 of these days each spider was given another fly during a second round of feeding.

The 8 populations were censused frequently. At each census all mature spiders were removed and measured. Very small spiders that were obvious immigrants were also removed. Censusing of all units

continued for 17 days after supplemental feeding had ceased, and on 14 September the experiment was terminated by removing and measuring all remaining spiders.

Rearing Field-Collected Juveniles

A major advantage of the field experiment was that biotic and physical factors that limit growth and development were at natural levels. However, because the populations were open the developmental fates of individual spiders could not be monitored without error. More direct evidence of the variable developmental fates of the progeny of spring adults was obtained by collecting spiders from natural populations and rearing them individually to the end of the season or until they had matured.

On 1 July 1980, 47 of the largest juveniles in the population were collected from Liberty. This collection included those offspring of spring adults most likely to complete development and reproduce that summer. In the following year a different sampling strategy was employed. In 1981, 89 of the smallest spiders (stages 1–3) in the Liberty population were collected on 6 July. These were the progeny of spring adults least likely to complete development within the season. I sampled the extemes of the size distribution in order to uncover the limits to the developmental potential of the population at a particular time. Logistical constraints prevented sampling of the entire range of size classes in a single season.

In 1982 juvenile spiders were collected from Liberty and Patuxent. As in 1981, the smallest spiders that could be found were removed, but they were collected two weeks later in the season. On 21 July I collected 41 immature spiders from Patuxent and 80 from Liberty. As in the previous two years, these spiders were also the progeny of spring adults, judging from the minimum time elapsing from maturity to hatching of progeny from the first egg sac (19–21 days; unpubl. data).

In all three years the collected spiders were reared in individual containers with a super-abundance of fruit flies. Although in nature the developmental rate of some juveniles might be limited by a shortage of prey, I provided a surplus of food in order to uncover the developmental potential of each individual. In 1980–81 rearings were done in the laboratory under natural photoperiod. In 1982 the juveniles were reared on the porch at Patuxent.

Statistical analyses of the results of all studies were done with the UCLA BMDP programs, converted for use on Cyber computers by the Northwestern University Computing Center.

Results

Phenological Patterns in Maryland Populations

Two peaks in adult abundance each season characterized the Liberty population (Fig. 1). Seasonal changes in the size-composition of both populations, particularly at Liberty, were similar to those found in the Michigan study (Figs. 2, 3; Wise 1976). The persistence of relatively high numbers of immature stages during the summer, and the absence of intermediate stages at the end of June, provide evidence of a polymorphic phenology: some progeny of the spring adults apparently over-wintered as juveniles, whereas others developed rapidly and molted to adulthood between the end of July and the first part of September. Average adult carapace width was always significantly smaller in summer than spring (Table 1), additional evidence that summer-maturing adults developed rapidly within a single season and were not the offspring of the previous summer's adults.

Females that matured in the spring laid more, but smaller, eggs than summer-maturing spiders (Table 1). Fecundity differences such as these could reflect different seasonally adaptive reproductive behaviors, or more simply, could have resulted entirely from reproductive parameters being correlated with female size. This possibility was examined. Analysis of the 1982 Patuxent data revealed statistically significant correlations between number of eggs in the first sac, egg diameter and female carapace width. Stepwise multiple linear regression of the pooled seasonal data indicated that number of eggs was significantly related to both female size and mean egg size ($R = .52$). Most of the variation in number of eggs laid could be explained by the correlation with carapace width; addition of egg size as an independent variable increased the value of R by only .05. In a similar analysis with egg size as the dependent variable, egg number was the only statistically significant independent variable. Seasonal differences in reproductive parameters were then re-examined by comparing the adjusted means through ANCOVA of the appropriate regression equations. Differences between spring

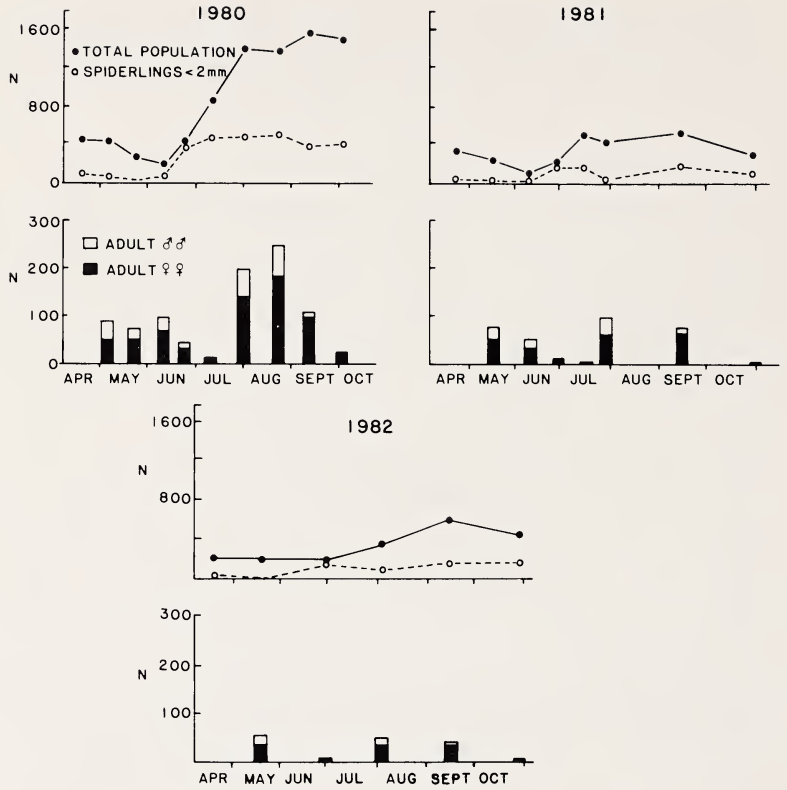


Figure 1. Seasonal and yearly changes at the Liberty site in density of spiderlings, adults and all stages combined. Numbers on the 13 marked areas are pooled. Changes in numbers are directly related to changes in population density because these same areas were censused each date. Although censuses were not conducted as frequently in 1982, they were made often enough to reveal a pattern similar to that of previous years: scarcity of adults at the end of June and an increase by early August.

and summer in number of eggs reflected seasonal differences in female size and egg size. However, the eggs laid by summer females were significantly larger than spring eggs even after correction had been made for the negative correlation with egg number (Table 2). The correlation between mean egg diameter and mean hatchling size for 46 summer females in 1982 was 0.51 ($p < .001$, $df = 44$).

The structures of the Liberty and Patuxent populations differed on the same date (Fig. 3). Peaks in adult abundance occurred earlier

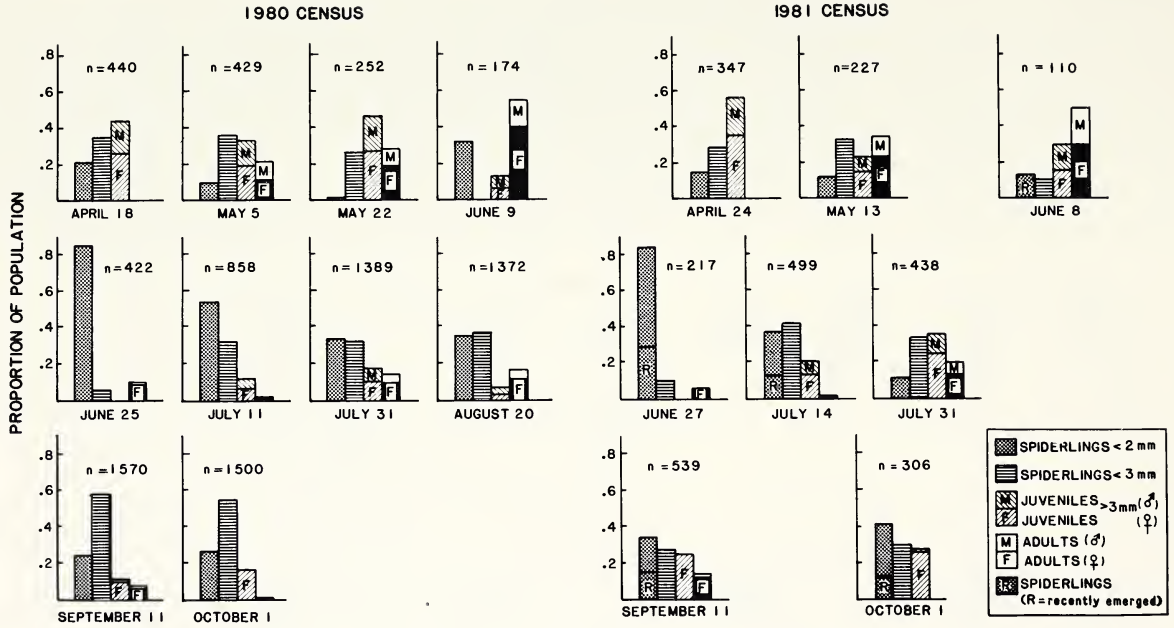


Figure 2. Structure of the Liberty population in 1980 and 1981. Recently emerged spiderlings (stage 1) were distinguished from larger ones < 2 mm in 1981 only. Length was estimated by eye, as spiders were left in the webs. All spiders categorized as juvenile males had noticeably swollen, but incompletely developed, pedipalps. Mature spiders were recognized with practically no error. For example, from August 1979 through August 1980, 84 of 85 females found in webs off the census areas that were judged to be adults were collected and verified under a microscope as being mature. The one mistake, a penultimate female, molted to the adult stage within a few days.

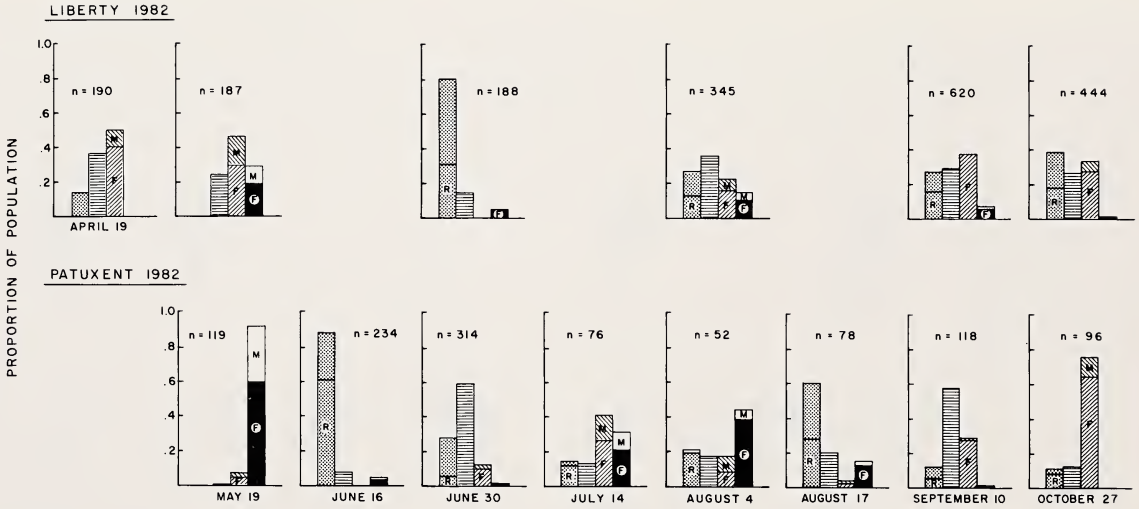


Figure 3. Structure of the Liberty and Patuxent populations in 1982. Same key as in Fig. 2. The Liberty population was censused less frequently in 1982 than was the one at Patuxent. Differences in numbers between the two populations do not reflect differences in density, because the total size of the 8 areas censused at Patuxent was smaller than that of the 13 Liberty areas. The Patuxent areas were marked in early June. Spiders scored to stage on 19 May at Patuxent were found by systematically searching other regions of the forest, and thus total numbers on 19 May cannot be compared to those of later censuses at Patuxent. Population structure, however, can be compared directly.

Table 1. Differences between spring and summer in size at maturity and reproductive parameters of spiders from Patuxent and Liberty populations. Means ± s.e. are given with sample sizes in parentheses. The Bonferroni Multiple Comparison Test was used to examine the significance of seasonal differences for the Liberty population in 1980, and for Patuxent in 1981 and 1982. Differences between spring and summer in carapace width, egg number and egg size were all significant at $p < .01$ or greater. Means did not differ significantly between areas within the same season and year. Means also did not differ significantly between years, with the exception of male carapace width in the Liberty population between the springs of 1980 and 1981 ($p < .01$).

		SPRING				SUMMER		
		Liberty		Patuxent		Liberty	Patuxent	
		1980	1981	1981	1982	1980	1981	1982
Females	Carapace (mm)	1.36	1.33	1.42	1.40	1.15	1.18	1.22
		±.01	±.01	±.02	±.01	±.01	±.01	±.01
		(52)	(27)	(35)	(93)	(52)	(71)	(48)
	Number of eggs,		63		66		50	49
	first sac		±6		±3		±3	±3
			(9)		(56)		(15)	(34)
	Egg diameter,	.610	.618	.597	.603	.653	.649	.641
	first sac (mm)	±.003	±.007	±.003	±.005	±.004	±.006	±.007
		(44)	(25)	(30)	(57)	(19)	(17)	(35)
Males	Carapace (mm)	1.57	1.47	1.55			1.29	1.25
		±.01	±.02	±.03			±.02	±.05
		(10)	(19)	(11)			(32)	(9)

in the season at Patuxent. For example, on 19 May 1982 only 30% of the Liberty population was mature, whereas at Patuxent over 90% were adults. Also, mature spiders comprised a greater proportion of the summer population at Patuxent, suggesting that more progeny of spring adults developed rapidly at Patuxent than at Liberty. At the end of the season more of the population consisted of older juveniles at Patuxent than at Liberty. The accelerated phenology of the Patuxent population may have resulted, at least partly, from warmer web-site temperatures at this lower-elevation site (Table 3). The relative proportion of adults in the population throughout the season at Liberty more closely resembled the pattern in Michigan than did the pattern at the Patuxent site.

Field Experiment

On Day 0 (21 July) a total of 238 immature spiders, stages 2–4, occupied webs on the units. By the middle of September the total

Table 2. Comparison of spring and summer fecundity parameters by ANCOVA. * = $p < .05$; ** = $p < .01$.

Number of Eggs in First Sac			
Source	D.F.	M.S.	F
Equality of Adj. Means	1	295	.82
Zero Slope	2	2305	6.45**
Error	79	357	
Equality of Slopes	2	730	2.10
Error	77	348	
Adjusted Means (± s.e.)—			
Spring: 61 ±3			
Summer: 56 ± 4			

Egg Diameter (mm), First Sac			
Source	D.F.	M.S.	F
Equality of Adj. Means	1	152.6	11.13**
Zero Slope	1	56.2	4.10*
Error	87	13.7	
Equality of Slopes	1	4.8	.34
Error	86	13.8	
Adjusted Means (± s.e.)—			
Spring: .606 ± .006			
Summer: .638 ± .007			

number of immatures occupying all eight units was slightly over 100 (Fig. 4). All appeared to be younger than the penultimate instar, judging from the absence of significant swelling of male palps and the undeveloped female external genitalia. During the experiment 39 very small juveniles were removed from the populations. These spiders were obvious immigrants, most likely the progeny of summer-maturing adults. The disappearance of immature spiders during August coincided with the appearance of adult males and females (Fig. 4). The rate of appearance of mature spiders of both sexes declined in September; no mature males appeared on the units after 1 September.

Supplementing the food supply did not affect numbers of immature or mature spiders on the units, nor did providing additional prey influence size at maturity. During the experiment mean numbers per unit and linear dimensions of removed adults were practically identical for the supplemented and control populations. Only 36 ± 2% of the spiders accepted the additional prey during the

Table 3. Web-site temperatures. Means ± s.e. with number of web sites measured in parentheses.

	Shady Sites		Sunny Sites	
	Patuxent	Liberty	Patuxent	Liberty
24 May	20.2 ± .2 (30)	18.6 ± .1 (57)	21.8 ± .6 (10)	19.6 ± .2 (4)
8 June	24.8 ± .3 (13)	23.5 ± .1 (54)	27.2 ± .4 (7)	24.1 ± .3 (14)

first feeding round each day, suggesting that the majority of immature spiders was not experiencing a shortage of prey.

Many adults that appeared during the experiment undoubtedly were immigrants, as were some of the juveniles present in September. However, a significant fraction of the immature spiders on the units in September was likely part of the original cohort, since small spiders that were obvious immigrants were removed continuously during the experiment. Clearly many adults were immigrants, as the number appearing exceeded the decline in number of immature spiders. However, substantial numbers of penultimate stages appeared on the units during the first few weeks, indicating that many of the adults did develop from spiders that had been added to the units. Thus the immature filmy dome spiders added to the units in July apparently had one of two fates. Some matured by August or September, whereas the remainder were still immature by the middle of September and would not mature until the following spring.

Rearing Studies: Field-Collected Juveniles

All 47 juveniles removed from the population at Liberty in 1980 had matured by the end of August. These appeared to have been stage 3 or older when collected on 1 July.

The following year not all survived to the end of the summer, probably because smaller instars were collected. Over half (65%) of the immatures collected in 1981 did survive, and all were adult by the end of August (Fig. 5).

In 1982 the populations were sampled 2 weeks later in July. Many of these juveniles had not matured by the end of the season. The total number that had either matured or were still alive as immatures by mid-September was 106 (86% of the number collected); 39% of these spiders were still immature. The developmental status

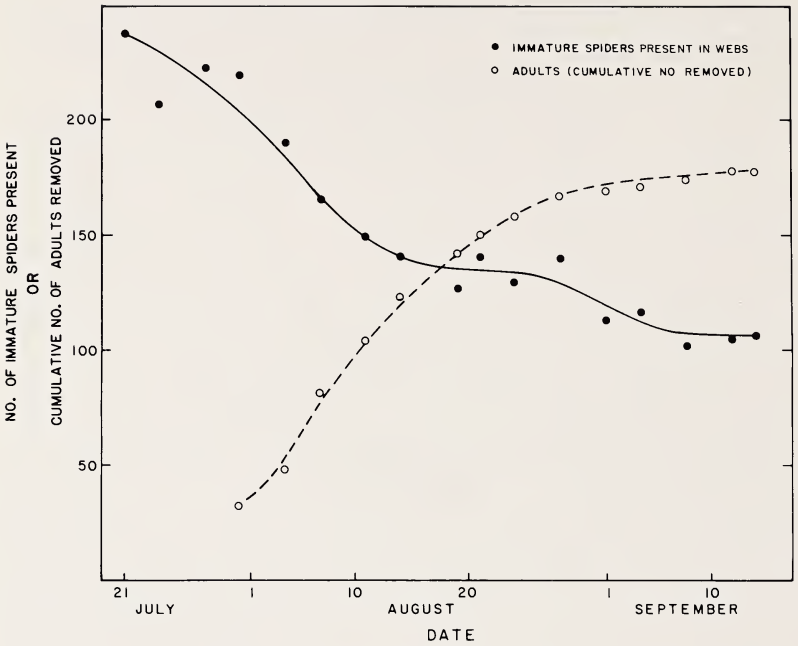


Figure 4. Numbers of immature spiders present in webs and cumulative numbers of adults removed during the 1981 field experiment. Not included are the obvious immigrants: juveniles smaller than those that were present the previous census (these were removed) and adults that appeared during the first week.

of spiders at this time of the season accurately predicts their state of maturity at the end of the season for two reasons: 1) In nature newly matured spiders do not appear after mid-September; 2) all but one of the immatures collected in 1982 that did mature that season completed the adult molt by 25 August. The one exception was a female that matured on 9 September.

When collected in July, juvenile spiders from Patuxent were more developed than those collected from Liberty and were more likely to have molted to adulthood by September (Fig. 6). A significantly greater proportion of the spiders from Patuxent was mature ($31/41 = .76$) than from Liberty ($34/65 = .52$) ($\chi^2 = 5.76$, $p < .05$). The mean date on which the spiders molted to the adult stage was 6 August for those from Patuxent and 15 August for the Liberty spiders. Although spiders that were larger when collected were more likely to have matured, the correlation with stage and future

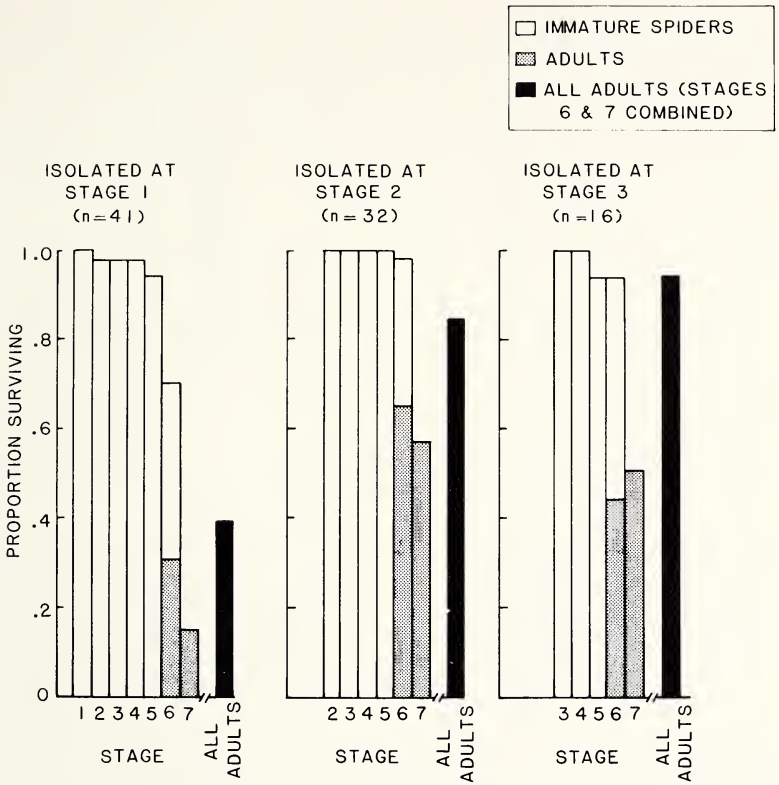
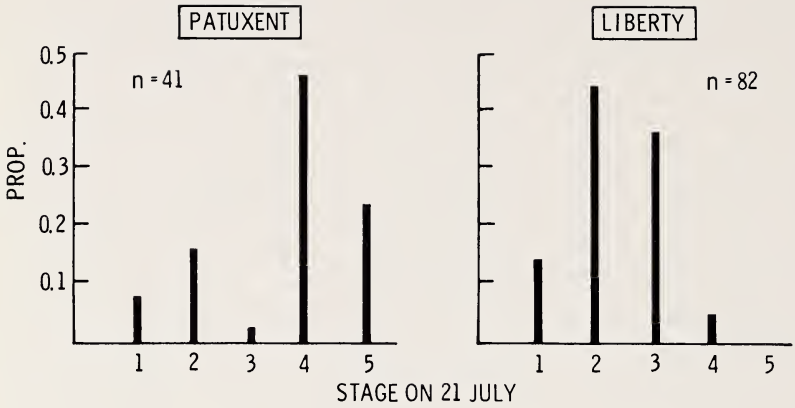


Figure 5. Development of immature spiders collected from the Liberty population on 6 July 1981 and reared in the laboratory. All had either matured or died by the end of August.

rate of development was not perfect. A few of the more advanced juveniles (≥ stage 3) survived but failed to mature during the 1982 season (Table 4).

Discussion

Maryland populations of the filmy dome spider exhibit a polymorphic life history pattern similar to that discovered in a more northern population in Michigan (Wise 1976). The phenology of the Liberty population more closely resembled that in Michigan than did the pattern at Patuxent, though data suggest considerable year-to-year variation at the latter site. This research has also furnished



DEVELOPMENTAL STATUS IN MID-SEPTEMBER:

	PATUXENT	LIBERTY
NO. MATURED	31	34
NO. IMMATURE (alive)	10	31
TOTAL (% of no. collected)	41 (100 %)	65 (79 %)

Figure 6. Development of immature spiders collected from the Patuxent and Liberty populations on 21 July 1982 and reared on the porch at Patuxent. The bar graph indicates the estimated stages of the spiders when collected. Below the graph is summarized the number of spiders that either had matured by mid-September or were immature and still alive at that time.

direct proof of the previously proposed interpretation of the observed phenology.

Causes of Variable Development in the Filmy Dome Spider

The life history variation existing within Maryland populations of the filmy dome spider does not result from a genetic polymorphism (Wise, submitted). Instead, most of the variation appears to be environmentally induced, resulting from the response of a plastic phenotype to variation in proximate limiting factors.

Laboratory studies of other spiders have demonstrated extensive phenotypic plasticity in developmental rate, size at maturity and fecundity in response to variation in food supply and physical con-

Table 4. Estimated stages, when collected from natural populations on 21 July 1982, of spiders that were alive as immatures in mid-September or that had matured by then. Stages were estimated by comparing tibia lengths to a distribution derived from a previous laboratory rearing study (unpubl). A. Numbers in each stage on 21 July that had matured. B. Numbers in each stage on 21 July that were immature and alive in September. All spiders that matured before winter had done so by mid-September.

	Stage in July				
	1	2	3	4	5
A. Matured					
Patuxent		2	1	19	9
Liberty		6	25	3	
Total		8	26	22	9
B. Immature					
Patuxent	3	5		1	1
Liberty	9	19	2	1	
Total	12	24	2	2	1

ditions (Browning 1941, Jones 1941, Deevey 1949, Turnbull 1962, 1965). Rearing studies with hatchlings of Patuxent females show that food supply can affect rates of growth and development of the filmy dome spider (Wise, submitted). Martyniuk has also demonstrated the plastic response of developmental rate in *N. radiata* to variations in prey abundance in a laboratory study, and in a field experiment has established that local differences in prey abundance influence web-site selection and tenacity in this species (Martyniuk 1983). Although the 1981 field experiment at Patuxent provided no evidence of food limitation, other research has demonstrated that natural prey levels can limit the fecundity and growth rate of filmy dome spiders in nature (Wise 1975). Differences in temperature between web sites also possibly contribute to intra-populational variation in developmental rate. Comparison of the phenologies at Patuxent and Liberty provides indirect evidence of the effect of temperature on developmental rate, since the stage of development was accelerated at the warmer location.

Environmentally induced variation in growth and development of filmy dome spiders partially explains their maturing at different times during the spring. In addition, seasonal selective constraints associated with the timing of reproduction by summer-maturing adults (to be discussed later) have apparently interacted with this variation to expand the spring reproductive period even further.

The result is a life history in which the timing of reproduction is the major variable determining the developmental patterns of the offspring.

In Maryland, spring-maturing *N. radiata* mate and lay eggs for 8–10 weeks, from May through early July. Offspring of these adults thus emerge from egg sacs over a considerable span of time. Spiderlings that hatch from sacs laid by early-maturing adults have time to complete development and reproduce before winter. Many of those that hatch from egg sacs laid at the end of the spring reproductive period have a different fate. While some may mature by the end of the season, not all develop that rapidly. Those that emerge from the later egg sacs, or that capture insufficient prey or construct webs at sites with low temperatures, over-winter as juveniles and become the early-maturing adults of the following spring. Populations exhibiting this life history pattern complete approximately three generations every two years.

The degree of polymorphism exhibited by a population appears to vary with the length and average temperature of the growing season. Almost all *N. radiata* at the Patuxent site completed two generations in 1982. However, at the higher, cooler Liberty site, and in the Michigan population studied previously (Wise 1976), a significant number of the offspring of spring females over-wintered as immatures and did not become adult until the next year. The summer peak of adults is reduced in *N. radiata* populations in the Catskill Mountains of New York (Martyniuk, pers. comm.). These patterns lead to the prediction that extreme southern populations of the filmy dome spider are consistently bivoltine, whereas populations at higher latitudes and elevations are univoltine. A substantial number of populations, perhaps most, likely show a life cycle that is intermediate between an annual and a biannual, or bivoltine, pattern.

The extent of the life history polymorphism may vary yearly at the same site, judging from experiences at Patuxent 1981–82. In the 1981 field experiment a substantial fraction of the spiders was still immature at the end of the season, yet in the following year very few progeny of spring adults failed to reach adulthood by August. In 1982 almost an entire day of searching at Patuxent was required to locate the 41 juveniles for the rearing experiment, yet in the previous year the earlier developmental stages had been much more abundant the same time of the season. Possibly this difference in age

structure resulted from poorer survival of the later egg sacs in 1982 compared to 1981, in addition to environmentally caused differences in developmental rates of hatchlings. These suggestions are speculative, as no data exist from which the causes of this particular yearly difference can be deduced.

Variable Phenologies in Other Spiders

Environmentally induced variable phenologies occur in other spiders (e.g. Dondale 1961, Almquist 1969, Toft 1976, 1983). Frequently this variation is correlated with differences in length and average temperature of the growing season, either between years or along latitudinal and elevational gradients. However, most examples involve shifts not between univoltine and bivoltine patterns, but between annual and biennial life cycles. In fact, the occurrence of two generations per year has not been reported often for spiders. Juberthie (1954) concluded that several species he studied had bivoltine life cycles, though his evidence came solely from laboratory rearings. At least one of the species that he studied apparently completes only one generation per year in nature (*Enoplognatha ovata;* Seligy 1971). However, examination of areas warmer than those studied by Seligy might reveal a biannual phenology for *E. ovata.* Bonnet (1930, cited by Levy 1970) found that *Pirata piraticus* probably produces two generations per year. Another wolf spider, *Lycosa T-insignita,* has a phenology similar to that of the filmy dome spider (Miyashita 1969). Two adult peaks occur, and as with *N. radiata,* adults that mature in the summer are smaller than spring-maturing individuals. Furthermore, apparently not all *L. T-insignita* complete two generations per year.

Possibly modified bivoltine life cycles are characteristic of many small spiders in temperate regions. Casual, non-systematic observations of the linyphiid *Frontinella pyramitela* (Walckenaer) suggest that this species may have two peaks in adult abundance each year (pers. obs.). The occurrence of two abundance peaks in a year, termed diplochronism by Tretzel (1961), occurs in several species of spiders (Toft 1976). However, Toft concluded that the phenomenon did not result from a mixture of biannual and annual life cycles for the species he studied in northern Europe, but instead occurred in species that had generation times of a year or longer. Conclusions about the ubiquity or rarity of both typical and modified bivoltine life cycles among temperate spiders must remain speculative until more evidence is gathered.

Adaptive Significance of N. radiata's Life History Plasticity

Is the life history plasticity exhibited by individual *N. radiata* adaptive? In discussing the adaptive significance of developmental plasticity, Smith-Gill (1983) distinguished between developmental conversion and phenotypic modulation. Passive response of the organism to environmental variation constitutes modulation, which is not necessarily adaptive. Continuous phenotypic variation frequently characterizes this type of plasticity. In *N. radiata,* non-adaptive phenotypic modulation is expressed as the variation in size at maturity and fecundity within spring and summer populations attributable to different feeding histories or web-site temperatures. On the other hand, the filmy dome spider's variable phenology apparently involves a developmental switch, and is likely an example of adaptive developmental conversion.

Several features of *N. radiata's* phenology argue against phenotypic modulation as the only explanation for the variable developmental rates exhibited by this species. One major feature supporting the argument against modulation is the presence of two pronounced peaks in adult abundance. It appears that individuals do not develop at similar rates during the season, with cold weather or changing photoperiod simply arresting development of all stages equally. That is, while variables such as temperature affect developmental rate, the effects apparently depend upon both the stage of the individual and the time of the season. Further support for developmental conversion comes from the timing of the summer peak in adult abundance. Not only do no adults over-winter, but nearly all summer-maturing spiders have completed the adult molt by the end of August. Furthermore, some spiders continue to grow and molt for many weeks after the last maturation ecdysis has occurred, eventually maturing the next season at a larger size than those that became adult in August. This pattern constitutes strong evidence that a developmental switch has occurred earlier in the season, either in the earlier instars or perhaps as a result of the type of eggs laid by late-maturing spring females. The developmental fates of juveniles collected at different times is also evidence that such a conversion from rapid to slower development occurs well in advance of the end of the season. Additional evidence comes from a rearing study that found marked differences in the developmental fates of hatchlings emerging at different times during June and July (Wise, submitted).

Perhaps adult *N. radiata* cannot adapt physiologically to cold. Thus winter mortality of adults might be one selective factor that has favored maturation well in advance of winter. Another possible selective factor might be the lower rate of survival over winter of smaller juvenile *N. radiata* (Martyniuk 1983; Wise, unpubl. data). The peak of egg-laying by the second generation occurs early enough for most hatchlings to emerge and complete one or more molts before the end of the growing season. Their chances of surviving the winter are greater than if they had emerged from egg sacs laid at the end of the season. Since egg size and hatchling size are positively correlated, the fact that summer females lay larger eggs than spring females also suggests the increased importance of size to juvenile survival later in the season.

Those spiderlings that postpone maturation tend to mature at a larger size, which leads to higher female fecundity. Increased size may also improve the mating success of males, since they compete aggressively for females (pers. obs.). These and other aspects of *N. radiata's* life history suggest that slower development is not unadaptive within the constraints seasonality imposes upon the timing of reproduction, and as part of a phenotype that also can develop more rapidly if environmental conditions are favorable. The hypothesis that the developmental plasticity of the filmy dome spider involves a developmental switch in the middle of the summer is tenable, but requires further testing. In particular, what are the proximate cues involved in the switch? Research on developmental rates of other spiders suggests that changing photoperiod may be important (Schaefer 1976, 1977). How do seasonal cues interact with the current physiological state and developmental history of the individual? What is the non-genetic maternal contribution to the developmental fate of hatchlings?

In addition to answering questions such as these, it would be fruitful to determine whether or not the type of developmental flexibility exhibited by *N. radiata* has evolved in other spiders. Such a life history pattern may be more widespread among temperate spiders than is now realized.

Summary

A polymorphic phenology, apparently characterized by rapid and slow developers among the progeny of spring-maturing adults, was found in two Maryland populations of the filmy dome spider, *N.*

radiata. Seasonal changes in the size-composition of the populations were similar to those found earlier in a Michigan population (Wise 1976). A field experiment and rearings of juveniles collected at different times of the season confirmed the presence of rapid and slow developers. Furthermore, these studies, in conjunction with the results of other research (Wise, submitted), established that variation in the timing of reproduction by spring-maturing females is the major contributor to the variable developmental rates of young spiders during the summer.

Progeny of early-spring maturing females develop rapidly, mature by August and deposit egg sacs before the end of the season. Hatchlings from these sacs over-winter as early instars and mature late the following spring. Progeny of these late-spring maturing individuals do not develop to maturity within the same season. Instead, these offspring over-winter as juveniles and mature early the next spring. On average, then, three generations are completed every two years in these populations.

These two paths of development represent two alternatives, determined primarily by the seasonal timing of reproduction, but subject to the influences of other environmental variables. Thus the pattern as described is idealized. The actual fraction of spiderlings developing along each path varies between sites, and even between years at the same site, in response to differences in environmental factors such as web-site temperature, length of the growing season and possibly prey abundance. In different situations anywhere from a few to most of the progeny of late-spring maturing individuals may develop to maturity in the same season that they hatched. Some northern populations of *N. radiata* may be mainly univoltine, whereas populations at the southern limits of the species' range may be entirely bivoltine.

The phenology exhibited by Maryland and Michigan populations of *N. radiata* is intermediate between an annual and a bivoltine life cycle. This type of phenology has not been reported often for spiders. Whether or not this pattern is unusual, or is common but undocumented, remains to be established.

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Submitted. Evidence that developmental plasticity rather than genetic variation causes the variable phenology of the filmy dome spider.

THE BEHAVIOR AND MORPHOLOGY OF THE FIG WASPS *PEGOSCAPUS ASSUETUS* AND *P. JIMENEZI*[1]: DESCRIPTIONS AND SUGGESTED BEHAVIORAL CHARACTERS FOR PHYLOGENETIC STUDIES

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Figs (*Ficus* spp., Moraceae) and their pollinator wasps (Agaonidae) are the most intricately coevolved of the plant-insect mutualisms. The necessity of the tiny wasps for good fruit set in cultivated figs [*Ficus carica* (L.)] was recognized over two thousand years ago by Aristotle and his pupil Theophrastus, and the details of pollination in this species were understood by the early part of this century (Condit 1947). It was only fifteen years ago, however, that the tremendous diversity in pollination mechanisms among the approximately 900 species of figs began to be appreciated (Ramirez 1969; Galil and Eisikowitch 1969; Chopra and Kaur 1969). It is generally accepted that each fig species is pollinated by a unique species of fig wasp (Ramirez 1970a; Wiebes 1979). There is much variability in fig inflorescence morphology, which is associated (by host specificity) with variability in fig wasp morphology (Ramirez 1974) and behavior (Galil and Meiri 1981). Although general trends in the mechanism of pollination across subtaxa of *Ficus* and Agaonidae can be inferred from fig inflorescence and fig wasp morphology (Ramirez 1974), the actual details of both pollen collecting and pollination by the wasps have only been studied in a few species. Among the monoecious figs, Galil and Snitzer-Pasternak (1970) studied the pollination of *Ficus religiosa* (L.) by the fig wasp *Blastophaga quadraticeps* (Mayr); Galil and Eisikowitch (1969, 1974) studied *F. sycomorus* (L.) and its pollinator *Ceratosolen arabicus* (Mayr); Joseph and Abdurahiman (1981) described pollination of *F. race-*

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mosa (L.) by *C. fusciceps* (Mayr); and Galil et al. (1973) observed the pollination of *F. costaricana* [(Liebman) Miquel] and *F. hemsleyana* (Standley) by *B. estherae* (Grandi) and *B. tonduzi* (Grandi), respectively. Among the dioecious figs, Galil (1973) reported on pollination of *F. fistulosa* (Reinw. ex Bl.) by *C. hewitti* (Waterston); Galil and Neeman (1977) described the details of pollen transfer and pollination in the edible fig *F. carica* (L.) by *B. psenses* (L.); and Okamota and Tashiro (1981) characterized a remarkable mechanism of pollen transport and pollination in *F. erecta* (Thunberg) by *B. nipponica* (Grandi).

The general features of the pollination cycle of monoecious figs have been described by Galil and co-workers (see above), and reviewed by Janzen (1979) and Wiebes (1979). In this paper I present a detailed description of the pollination cycles of *Ficus aurea* (Nuttall) and *F. citrifolia* (P. Miller), which are pollinated by the fig wasps *Pegoscapus jimenezi* (Grandi) and *P. assuetus* (Grandi), respectively (see Wiebes 1983 for taxonomic discussion of these fig wasp species). The two fig species are closely related members of the monoecious section *Urostigma*. New information presented in this paper includes detailed scanning electron micrographs of the morphology associated with pollination by *Pegoscapus jimenezi,* and detailed descriptions of the behavior during entry into the fig inflorescence, during pollination, and during pollen collecting by *P. jimenezi* and *P. assuetus* in Florida. These behaviors are very similar to those described by Galil et al. (1973) in Costa Rica for the fig wasps *Blastophaga* (=*Pegoscapus*) *estherae* and *B. tonduzi,* which pollinate *Ficus costaricana* and *F. hemsleyana,* respectively. However, clear differences in behavior exist between the fig wasps discussed in this paper and the descriptions of the two Costa Rican species. The usefulness of these behavioral characters for the study of fig wasp phylogeny will be explored in the discussion.

Methods

This study was conducted in the Everglades National Park during June 1981. Observations of entry behavior were made in the field with a hand lens. Observations of pollination and pollen-collecting behavior were made by collecting figs at the appropriate stage (see next section), taking the figs into the lab and slicing them open, and observing the wasps with a dissecting microscope. Since no morpho-

logical or behavioral differences relevant to pollination were noticed between the two species studied, the descriptions that follow apply to both fig wasp species.

Observations

The details of the flowering and pollination cycle of *Ficus citrifolia* and *F. aurea* will be described in this section. The cycle is presented according to the stages of development of the fig inflorescence (syconium).

Early Development of Syconium and Entry by Pollinator Wasps

A monoecious syconium is a globular inflorescence containing hundreds of pistillate and fewer staminate florets that line a sealed cavity. The only entrance into this cavity is a series of closely packed, overlapping scales called the 'ostiole.' The young syconia first appear singly, or in pairs, as small protrusions in the leaf axils. Syconia of *F. citrifolia* develop a peduncle 0.5–1.5 mm long, while syconia of *F. aurea* are sessile and subtended by basal bracts. During the early stages of syconium development, the ostiole of *F. aurea* is hidden by two bracts that envelop the entire syconium, while ostiolar scales of *F. citrifolia* are exposed but remain tightly packed, thereby preventing entry by the wasps. As the pistillate florets in the syconia mature, the ostiolar scales of *F. citrifolia* loosen, and the enveloping bracts of *F. aurea* spread to reveal the ostioles. At this stage syconia of *F. citrifolia* are 5–8 mm in diameter, and syconia of *F. aurea* are 4–6 mm in diameter. The syconia are now ready to be entered by the pollinator wasps. Circumstantial evidence suggests that the trees emit a species-specific chemical attractant that indicates receptive syconia (Frank 1983a). Experimental evidence suggests that the pollinator wasps *Pegoscapus assuetus* (reared from *F. citrifolia*) and *P. jimenezi* (reared from *F. aurea*) distinguish between the two fig tree species and, except for rare events, will only enter their own host tree species (Frank 1983a).

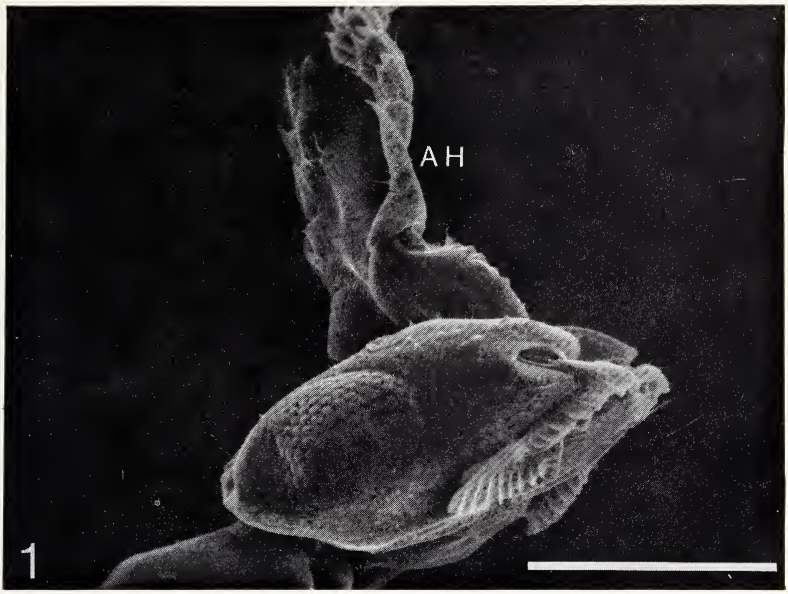
The wasps' entry into the syconia is a fixed sequence of behavioral events. A female pollinator wasp (1.2–1.8 mm in length) arrives at and immediately begins antennating a syconium. The wasp assumes a characteristic pose during this "assessment behavior." The legs are extended and the head and sternum are well clear of the syconium surface. The antennae are arched up and the distal portion of the antennae contact the syconium surface perpendicularly, with only

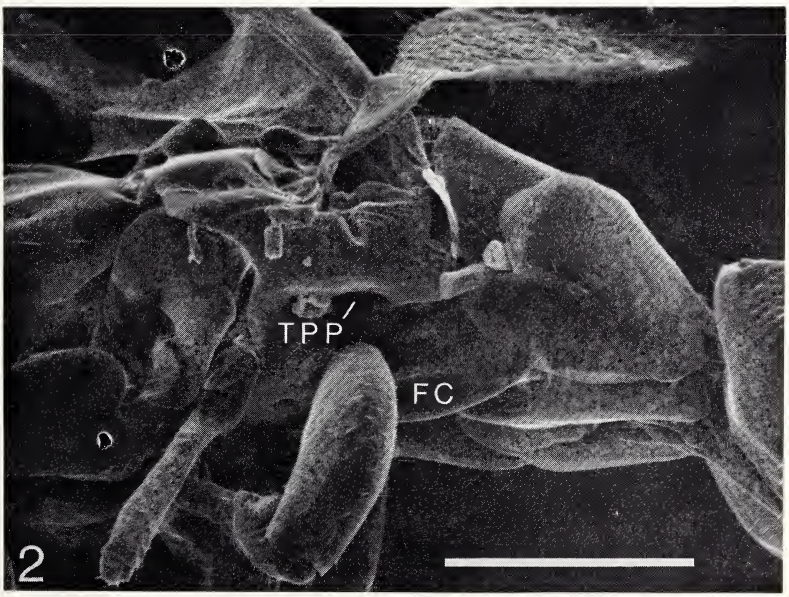
the distal antennal segment actually touching the syconium. The wasp walks over the surface of the syconium in this manner, and does not seem to follow any discernable pattern of movement (such as spending more time near the ostiole). The assessment period lasts from a few seconds to more than five minutes. After assessment the wasp may walk off the syconium and search for other syconia on the same branch, fly away, or begin the next phase of entry.

If the wasp attempts entry, she lowers her antennae, and the distal five or six antennal segments are pressed flat against the syconium surface. The wasp is searching for the ostiole, which she recognizes as a lip on the smooth syconium surface. When she finds the ostiole she loosens the topmost scale with one of the sharp, sclerotized horns on the third antennal segment (Fig. 1). If the upper scale is stuck to the tissue layer below, as is often the case on syconia that have not yet been entered, she approaches at an angle, hooks one horn under the scale, and works the scale free by pushing up with her forelegs and head. When the scale is loosened, she is ready to begin entry. The legs are spread laterally from the body, and the ventral surface of the entire body is flattened against the syconium surface. The antennae are forward and also pressed against the syconium; the wings are raised perpendicularly to the thorax and pressed together; and the abdomen, which has a flexible pleural region and mobile tergites and sternites, is compressed dorsoventrally. The wasp now pushes her antennae and head under the topmost scale of the ostiole. As the wasp pushes her way forward she arcs her body at approximately a 120° angle. She slowly disappears, and as her thorax passes through the topmost scale her upraised wings detach. When several wasps enter a single syconium, a tuft of wings can be seen at the entrance to the ostiole. As the female passes under the top scale, she contacts and pushes her head under the lip of the second scale, and continues walking the helical ostiole. The antennae distal to the fourth or fifth segment detach during entry. Also, it has been reported that the unusual mandibles (Fig. 1) are used to aid in entry (Ramirez 1970b). Wasps are not always successful at passing through the ostiole, and are sometimes found dead within the scales of the ostiole, frozen in the remarkably flattened attitude taken during entry.

Female Phase of Syconium; Oviposition and Pollination by Wasps

After wasps arrive in the central cavity of the syconium they oviposit and pollinate during the day or two before they die. At this





Figures 1 and 2. *Pegoscapus jimenezi.* AH = antennal horn, FC = forecoxa, TPP = thoracic pollen pocket. Bar is 150μm.

stage the pistillate florets are mature and the staminate florets are small and not fully developed ('female-phase' according to Galil and Eisikowitch 1968). The stigmata are intertwined to form a continuous mat (synstigma) that lines the inner surface of the spherical cavity. During entry into the syconium the hypopygium (a movable, sclerotized plate) is flush against the ventral surface of the abdomen, and the abdomen is flattened dorsoventrally. With her rear legs the wasp now kicks the hypopygium down perpendicular to the abdomen (position of hypopygium as in Fig. 16 of Galil and Eisikowitch 1969), and the abdomen becomes slightly compressed laterally. She also uses her rear legs to move the ovipositor shaft from within the ovipositor valves, which protrude distally from the abdomen, to a perpendicular position braced against the triangular hypopygium. The rear legs are also used to groom the ovipositor shaft. When the positioning of the ovipositor is first accomplished the tip of the ovipositor shaft protrudes just beyond the tip of the of the hypopygium. The female is now prepared to oviposit, and searches by probing the stigmata with the tip of her ovipositor. Eggs are laid by extending the ovipositor down the style and into the ovary of a pistillate floret, where the larva will develop while feeding on the tissues associated with the developing seed or on the seed itself. Within these fig inflorescences there is polymorphism in style length among the pistillate florets. The fig wasp's ovipositor is long enough to reach down shorter-styled florets and into the ovary, but is usually not long enough to reach down longer styles and into the ovary. Thus the short-styled florets usually produce wasps, while the long-styled florets usually produce seeds. While ovipositing the wasp stands on all six legs, with the body and head well clear of the stigmata, and the tip of the hypopygium just touching the top of the stigma being oviposited in. Oviposition lasts 105–300 seconds (n=9).

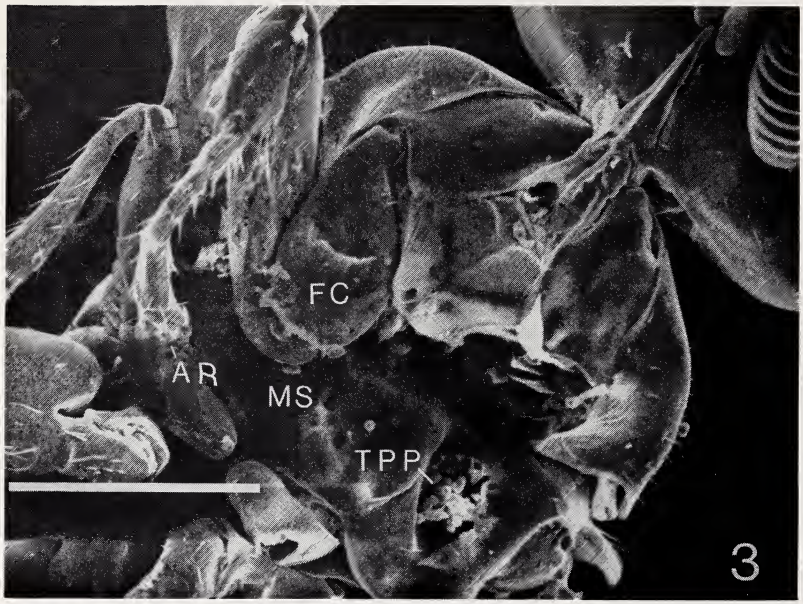
The wasps usually spread pollen nearby after each oviposition. Pollination consists of four behaviors: (i) loosening a few pollen grains from the caches kept in special sternal mesothoracic pockets, (ii) collecting these loose pollen grains in scoopers (arolia) on the foretarsi, (iii) transferring the pollen from the arolia to the surface of the hypopygium, and (iv) dragging the pollen-dusted hypopygium over the stigmata.

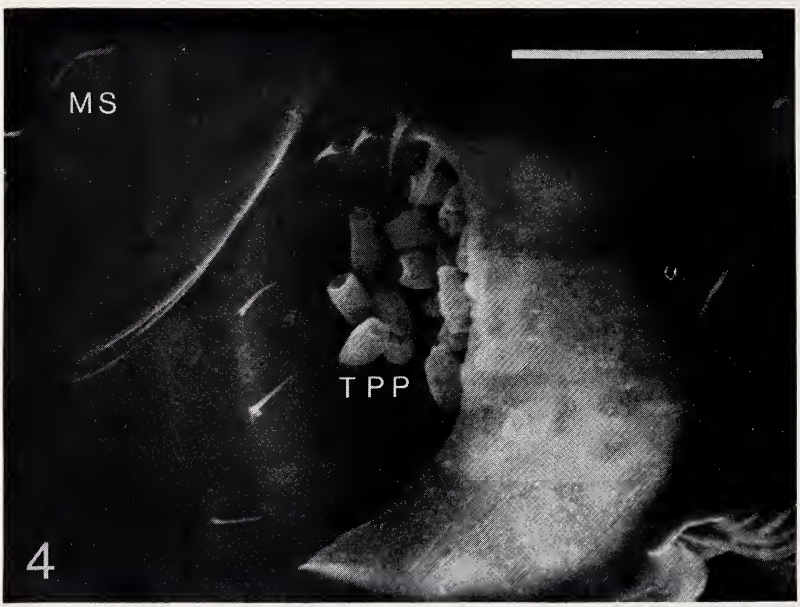
(i) Loosening pollen from the thoracic pockets. Towards the end of an oviposition act the wasp lifts her forelegs and begins a rhythmic motion with the front part of her body. The pronotum and head

slide forward and down—the pronotum dropping about 70° from horizontal while sliding over the mesonotum as an airplane-wing flap. The forecoxae move up flush against the mesosternum (Figs. 2,3); simultaneous with the pronotum and head moving forward and down, the forecoxae slide posteriorly then laterally over the mesosternum. First the forecoxae are moved back so that they are medial to the pollen pockets, which are located laterally on the mesosternum (Figs. 3,4). (These pockets are loaded with pollen; the manner in which the wasp obtains this pollen is described in the next section.) The forecoxae are then moved laterally until they are over the pollen pockets, and a stiff row of bristles on the coxal-femoral joints is at the posterior ends of the pockets (Figs. 5,6). The wasp then moves her pronotum and head up and simultaneously slides the coxae forward through the pockets. This causes the coxal-femoral bristles moving through the pockets to act as rakes, which loosen a few pollen grains and move them to the forward edge of the pockets. An alternative interpretation of the action of the coxal rake is that it scoops pollen out of the mesothoracic pockets and into the coxal pockets (corbiculae, Fig. 7). The two interpretations are discussed below in (ii).

(ii) Collecting pollen grains in arolia. After pollen is loosened from the mesothoracic pockets, the tibiae are quickly moved upwards until they are flattened against the femorae, such that both the tibiae and femorae are parallel to the stigmatal surface and pulled in close to the body. The arolia at the tips of the foretarsi open into membranous scoops, and are very quickly brushed back and forth 3–5 times (n=6) in order to collect pollen. It is difficult to observe exactly where the pollen is collected. On three occasions I saw an arolium scoop pollen from the front edge of a thoracic pocket. In the remainder of my observations (approximately 50 occasions) I was unable to determine whether the arolium obtained pollen from within or near the thoracic pocket, or from the coxal pollen pockets, as reported for *Blastophaga estherae* and *B. tonduzi* by Galil et al. (1973). Based on the structure of the coxal rake (Figs. 5,6) and pattern of movements in (i), and my observations, I favor the interpretation that the pollen is usually collected by the arolia in or near the mesothoracic pockets.

(iii) Transferring pollen from arolia to hypopygium. After pollen is collected in the arolia, the wasp reaches down with her forelegs and wipes the arolia upwards along the anterior edge of the hypopy-





Figures 3 and 4. *P. jimenezi*. FC = forecoxa, TPP = thoracic pollen pockets, MS = mesosternum, AR = arolium; note lateral pocket membrane in Fig. 4. Bar is 150μm in Fig. 3, 40 μm in Fig. 4.

gium, this plate being in the down position, perpendicular to the abdomen.

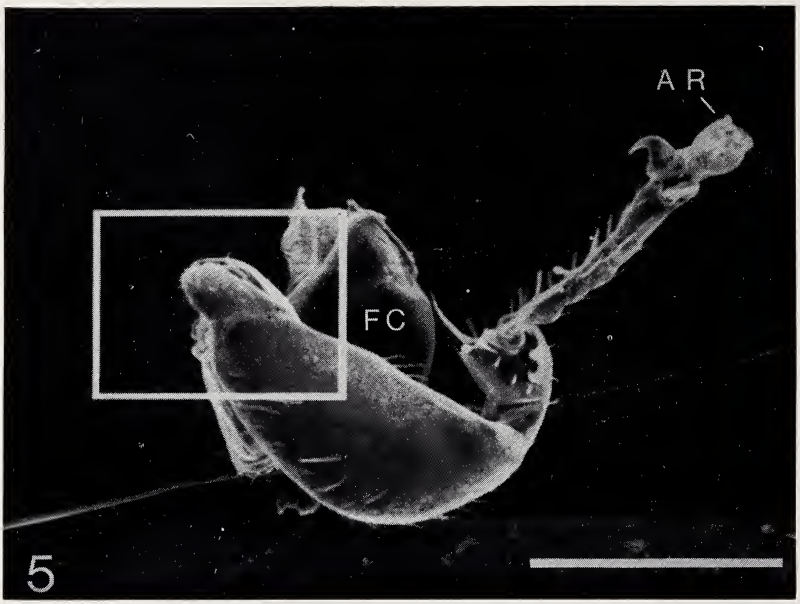
(iv) Dragging the pollen-dusted hypopygium over the stigmata. The tip of the hypopygium is kept just above the stigmatal surface during oviposition, and during steps (i)–(iii) described above. After being dusted with pollen from the arolia, the tip of the hypopygium is pushed down into the stigmata as the wasp begins to walk and search for a new floret in which to oviposit. Time spent searching between pollination and the beginning of the next oviposition ranged from 15 seconds to 150 seconds (n=5).

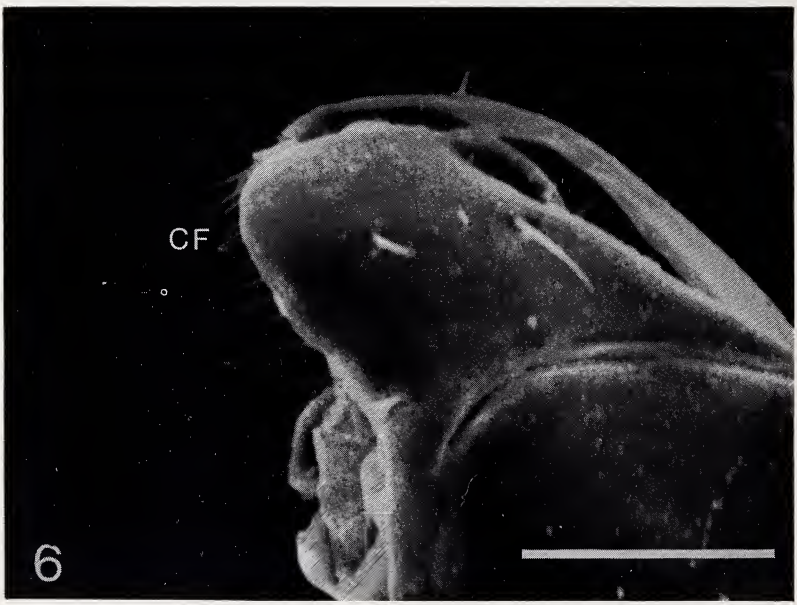
Two or more wasps often oviposit and pollinate simultaneously within a syconium (Frank 1983a). Among the approximately one hundred syconia I opened with two or more wasps ovipositing simultaneously, I never observed any sort of behavior that might be called 'aggressive.' Ramirez (1970b) has reported that New World fig wasps are aggressive towards each other during oviposition and pollination, but he did not specify in which species he actually observed aggressive behavior.

After females of *P. jimenezi* lay 23–130 eggs each (n=9), or females of *P. assuetus* lay 9–110 eggs each (n=18) (Frank 1983a), the wasps die in the central cavity of the syconium. The larvae and seeds develop—this period is referred to as the 'interfloral phase' of syconium development (Galil and Eisikowitch 1968).

Male Phase of Syconium; Mating and Pollen Collecting by Wasps

After 27–32 days the central cavity swells. The staminate florets are now mature (hence 'male phase' according to Galil and Eisikowitch 1968), and the randomly located anthers are clearly visible within the cavity. The male progeny emerge from the ovaries of the pistillate florets in which they developed. The percentage of males among the progeny generation is much less than the percentage of females (typically 5–20% males). Further, there is a strong positive correlation in *P. assuetus* between the number of females ovipositing in a syconium and the percentage of males in the progeny generation (Frank 1983a,b). The wingless males have reduced eyes and little pigmentation. Their legs are short and thick, and their abdomens curl under the ventral surface of the thorax and head (Fig. 8). The males wander through the labyrinth-garden of swollen pistillate and now mature staminate florets, searching for females. These females are mature, but remain quiescent in the floral ovaries in





Figures 5 and 6. Right foreleg of *P. jimenezi*. AR = arolium, FC = forecoxa, CF = coxal-femoral rake. Fig. 6 is an enlargement of the box in Fig. 5. The bar is 150μm in Fig. 5, 30μm in Fig. 6.

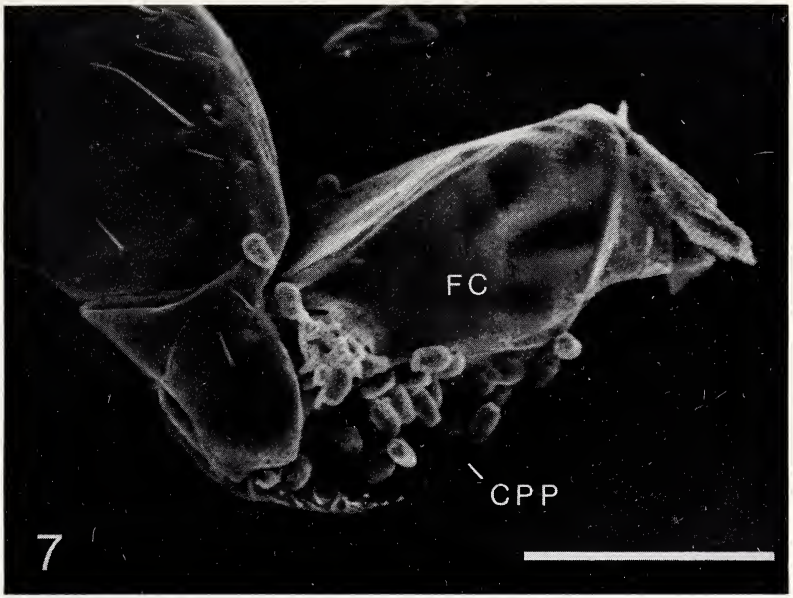


Figure 7. Left foreleg of *P. jimenezi*. FC = forecoxa, CPP = coxal pollen pocket. The bar is 60μm.

Figure 8. Male of *P. jimenezi*. Bar is 400μm.

which they developed. When a male finds an ovary containing a female, he chews a hole, inserts his telescoping abdomen, and mates with the female. The many males within the confined cavity walk into, over, and on top of each other, but I know of no report of aggressive interactions among male fig wasps. Nonrandom patterns of male movement within the syconium during mating have been discussed by Frank (1983a, 1985).

After a one to two day mating period, one or more males chew(s) an exit tunnel through the wall of the syconium. Following completion of the exit tunnel, the females widen the hole in the floret ovary created by the male during mating, and then struggle free into the central cavity of the syconium. Their wings are stuck to the abdomen and the pupal skin still covers their heads. They quickly groom their wings free by passing their rear legs between the wings and upper abdomen while simultaneously removing their pupal skin from their head with their forelegs.

After grooming, the females immediately begin to search for an anther that still contains pollen. When an anther is found the dehiscence slit is opened by passing one of the sclerotized horns on the third antennal segment (Fig. 1) through the length of the slit. Then the anterior portion of the head is placed within the anther, with the mandibles loosening the pollen grains, and the pronotum is slid forward and down. Next a foreleg (e.g., right foreleg) is stretched forward and placed in the anther, and the arolium scoops up a load of pollen. This load of pollen is moved upwards to the left forecoxa, and the left foreleg is simultaneously extended towards the anther. As the left foreleg is extended the left coxa is moved slightly away from the underside of the body exposing the pocket on the coxa (Fig. 7). The load of pollen from the right arolium is placed in the pocket of the left coxa. Next the right foreleg is extended again to pick up another load of pollen, and the pollen load of the left foreleg is placed on the right coxal pocket. After 16–32 loads (n=7) have been collected, the coxal pockets are bulging with pollen. Pollen is also in the intersegmental region between the pro- and meso-sterna.

The pollen is now moved from the coxal pockets and sternal region to the mesothoracic pockets. The sequence of movements is quite similar to those described above for pollen raking during pollination. The wasp lifts her head from the anther. The coxae are pressed against the prosternum, forming about a 45° angle with the medial line of the sternum. The coxae are then brushed posteriorly

across the intersegmentus, while maintaining their angle relative to the median sternal line. This movement of the coxae is accomplished by sliding the pronotum forward and down, which causes the prosternum to form about an 80° angle with the mesosternum. The coxae are now against the flattened medial region of the mesosternum (Fig. 3). Next the coxae are brushed laterally over the mesothoracic pockets (Figs. 9,10). The lateral membranous flap of the pockets (Fig. 4) may aid in scooping the pollen from the coxal pockets. The coxae are brought forward again when the pronotum is raised; thus the coxae are moved in a circular motion. The sequence is usually repeated 3–8 times, although the observed range was 2–34 (n=15). Sometimes two or three females will collect pollen from the same anther. If only a small amount of pollen is collected, the wasp will find another anther and repeat the pollen collecting sequence.

After collecting pollen the wasps leave the syconium through the exit tunnel and quickly take to the air, perhaps because predaceous ants of the genus *Pseudomyrmex* are often waiting for escaping wasps. Those wasps that successfully find receptive syconia begin the cycle again.

Discussion

The use of behavioral characters in systematics has been reviewed and discussed several times (e.g., Lorenz 1950; Evans 1952; Mayr 1958; Alexander 1962; Blair 1962; Atz 1970; Hinde 1970). Three examples are Lorenz's (1941) phylogeny of ducks and geese (Anatidae) based solely on behavioral characters, leading to Delacour and Mayr's (1945) revision based on both morphology and behavior, Evans' (1952) work on the comparative behavior and systematics of spider wasps (Pompilidae), and van den Assem et al.'s (1982) subdivision of *Melittobia* (Eulophidae) based on mating behavior. Also, several workers have noted a reasonable congruence between inferred phylogenies based on behavior and those based on morphology (e.g., Speith 1952 for *Drosophila;* Crane 1952 for mantids; and Michener et al. 1978 for Apidae).

The phylogeny of the Agaonidae is controversial (Wiebes 1982), and much work remains. Behavioral characters have not been used in fig wasp systematics, simply because there is not enough comparative information available. Fig wasps seem ideal for comparative studies of behavior, since so much of their behavior is extremely

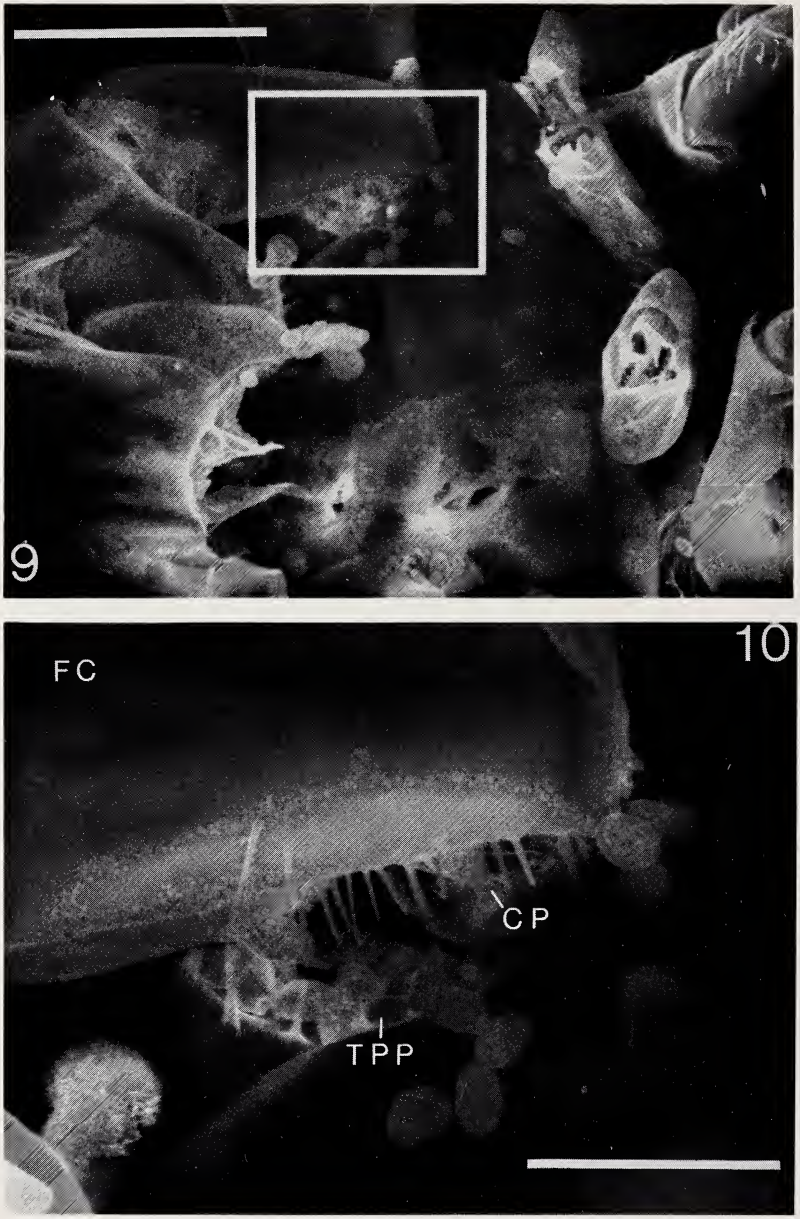


Figure 9 and 10. Pro- and meso-sterna of *P. jimenezi*. TPP = thoracic pollen pocket, FC = forecoxa, CP = coxal pollen brush. Fig. 10 is an enlargement of the box in Fig. 9. The bar in Fig. 9 is 100μm, 30μm in Fig. 10.

stereotyped and easily observed, and since the wasps' morphological structures make sense only in light of their associated motor patterns. Based on the few species reviewed below, it seems that behavioral information will be of some value in sorting out the systematics of this difficult group.

The sequence of behaviors during pollen collecting and during oviposition and pollination are compared in Table 1 between the Florida wasps *Pegoscapus assuetus* and *P. jimenezi* and the Costa Rican wasps *P. tonduzi* and *P. estherae*. There are three reasons for presenting this comparison. First, it highlights the extreme similarity in behavior among these four species. Second, it points out that clear differences in behavior do exist, and that these differences may be good characters for phylogenetic inference, or at least that a congruence between established phylogenies and behavioral differences may be observed (see also Table 2). Finally, these comparisons show the sort of detailed description that will be necessary if behavioral characters are to prove valuable, and will hopefully stimulate fig-watchers to begin assembling the necessary comparative information so that this story of morphological and behavioral coevolution can be written.

Acknowledgments

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Table 1. Comparison of oviposition and pollination, and of pollen collecting between *Pegoscapus assuetus* and *P. jimenezi* (described in this paper) and *P. tonduzi* and *P. estherae* (Galil et al. 1973). All these wasps pollinate figs of the monoecious section *Urostigma*. These descriptions are schematic and are only meant to highlight obvious similarities and differences. See original descriptions for more details.

Pegoscapus assuetus and *P. jimenezi*

OVIPOSITION AND POLLINATION: Probe synstigma with ovipositor → insert ovipositor down style → oviposit → loosen pollen grains in mesothoracic pockets with coxal-femoral rake → collect pollen in arolia from thoracic or coxal pollen pockets[1] → wipe pollen from arolia onto hypopygium[2] → drag hypopygium over synstigma.

POLLEN COLLECTING: slit anther with antennal horn → place anterior portion of head in anther → [right arolium scoops pollen from anther[3] → right arolium pulled towards ventral surface of body, left arolium simultaneously extended → left arolium scoops pollen from anther, right arolium simultaneously places pollen load on exposed left coxal pocket →right arolium extended to scoop pollen load from anther, left arolium simultaneously places pollen load on exposed right coxal pocket] → repeat brackets 16–32 (n=7) times → forecoxae rubbed posteriorly over mesosternum, then laterally over mesothoracic pollen pockets, transferring most of pollen to these pockets.

Pegoscapus tonduzi and *P. estherae*

OVIPOSITION AND POLLINATION: Probe → insert → oviposit → loosen pollen → collect pollen into arolia[1] → release pollen by rubbing arolia together above (not touching) synstigma[2].

POLLEN COLLECTING: slit anther → head in anther → arolia alternately lift pollen (up to 40 times) towards ventral surface of thorax → some pollen pressed into intersegmental chamber by forecoxae → coxae rubbed over mesosternum and pollen pockets, filling mesothoracic pockets, repeated several times.

[1]It is not known whether the arolia usually collect pollen from the thoracic pockets, or from the coxal pockets. My interpretation of *P. assuetus* and *P. jimenezi* is that pollen is taken directly from the thoracic pockets; Galil et al. (1973) suggest that the arolia collect pollen from the coxal pockets in *P. tonduzi* and *P. estherae*.

[2]This is the clearest difference between the two pairs of species.

[3]Choice of the right foreleg instead of the left is arbitrary, and only for purposes of illustration.

Table 2. Comparison of oviposition and pollination, and of pollen collecting, between *Ceratosolen arabicus* (Galil and Eisikowitch 1969, 1974), *C. hewitti* (Galil 1973), and *C. fusciceps* (Joseph and Abdurahiman 1981), and *Blastophaga quadraticeps* (Galil and Snitzer-Pasternak 1970). These descriptions are schematic and are only meant to highlight obvious similarities and differences. See original papers for more details.

Ceratosolen arabicus, C. hewitti[1], and *C. fusciceps*

OVIPOSITION AND POLLINATION: Probe synstigma with ovipositor → insert ovipositor down style → oviposit and simultaneously tremble and lower head to vigorously bite the stigmata within reach → forelegs lifted, forecoxae pressed to thorax → [femur and tarsi become parallel, and are moved together downward and posteriorly → when femur-tarsi are at right angles to coxae, arolia are moved into open pocket and collect pollen] → repeat brackets several times → tarsi are unfolded downward and touch stigmata → retract ovipositor → repeat entire cycle.

POLLEN COLLECTING: Pollen pockets have membranous covers, as opposed to open pockets of *Pegoscapus* spp. (see Fig. 4). Male wasps detach anthers → females emerge from flowers in which they developed → grasp anther → search for dehiscence slit → widen slit with mandibles and antennae → pollen lifted from anther to underside of thorax with arolia (32–98 alternate lifting, n=3) → thorax curved so that covering membranes of thoracic pockets stand out → pollen pushed into thoracic pockets with combs on forecoxae → males chew exit tunnel → females leave fig.

Blastophaga quadraticeps

OVIPOSITION AND POLLINATION: As in *C. arabicus,* except body is almost static during oviposition, head is motionless and no biting of synstigma occurs.

POLLEN COLLECTING: Pockets have membranous covers. Male wasps chew exit tunnel → females emerge from flowers in which they developed → approach anther → crumble pollen with base of antennae and mandibles → forelegs touch anthers, then move up and back along inner margin of thoracic pocket, repeated several times, motion identical to reverse of pocket unloading in *C. arabicus* → leave fig through exit tunnel with thoracic pockets full of pollen.

[1] *C. hewitti* pollinates a dioecious fig, while the other three wasps described here pollinate monoecious figs.

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RELATIONSHIPS AMONG PHILOTARSID AND PSEUDOCAECILIID GENERA AND A PROPOSED NEW FAMILY BRYOPSOCIDAE (PSOCOPTERA)*

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Introduction

In the classification of any group of organisms, views that have a long tradition are often difficult to put aside. We may weight certain characters heavily out of respect for such a traditional view. Weighting may even become an unconscious act if we uncritically include a particular character in the definition of a taxon. The character, then, comes to have absolute weight in our subsequent decisions about which subtaxa will be placed in the taxon and which will not. One must remember, however, that taxa, being constituted by organisms, have the capacity to evolve, and that any one character may have changed (evolved) in a subtaxon while others have not. We must not let a group definition come in the way of showing true relationships.

There has generally either been implied or expressed the view that adults in the psocopteran family Philotarsidae have three tarsomeres (Pearman 1936, Badonnel 1951, Smithers 1972, Thornton 1981). For some time, this was an indisputable fact, but Mockford and Evans (1976) and Mockford and Broadhead (1982), assigned species with two tarsomeres to this family.

Various authors have noted that adults in the family Pseudocaeciliidae have two tarsomeres (Pearman 1936, Badonnel 1951, Lee and Thornton 1967). This view remained unchanged until Meinander (1978) assigned a genus with three tarsomeres to this family. It appears now that adherence to the traditional view that Philotarsids should have three tarsomeres and Pseudocaeciliids should have two has led to a rather serious error in classification.

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In a series of papers, Thornton and co-workers (Thornton and Smithers 1974, 1977, 1978, Thornton and New 1977a, b, Thornton, Wong, and Smithers 1977) have described numerous species of Philotarsidae from Australia, New Zealand, New Guinea, New Caledonia, and surrounding islands. Following these works, Thornton (1981) presented a classification of the Philotarsidae.

In an earlier work, Lee and Thornton (1967) described numerous species of Pseudocaeciliidae from southeastern Asia and the Islands of the South Pacific. If one compares the figures in this paper with figures for the Philotarsid genera *Zelandopsocus* and *Austropsocus* in the papers cited above, one sees numerous points of marked similarity.

Methods

The observations of notable similarities between two Philotarsid genera and several Pseudocaeciliid genera led me to make a comparison of as many of the genera of both families as the literature and material at hand allow (Table 1). Comparisons were made of 11 characters. All of those chosen hold constant (i.e., in the same state) in more than one genus but fewer than all genera of the assemblage. Therefore, they may be expected to hold information about relationships among these genera. Among characters which qualify in this way, the ones chosen are easily defined, and most of them have been described and/or figured in recent taxonomic works. Illustrations (Figs. 1–3) are included for characters which require them.

Results and Discussion

In eight of the characters, both *Austropsocus* and *Zelandopsocus,* with three tarsomeres, agree with the Pseudocaeciliid genera. In presence of only a single row of setae on the M-Cu stem in the forewing, *Zelandopsocus* agrees with the other Philotarsid genera, while *Austropsocus* agrees with the Pseudocaeciliid genera. In the lateral tyne of the lacinial tip, *Zelandopsocus,* from published figures, appears to be intermediate between the other Philotarsids and the Pseudocaeciliids (but observation of *Z. cumulus* Thornton and New indicates closer proximity to Pseudocaeciliids), while *Austropsocus* agrees with the Pseudocaeciliids. *Bryopsocus* agrees with the other Philotarsids in five characters, with the Pseudocaeciliids in

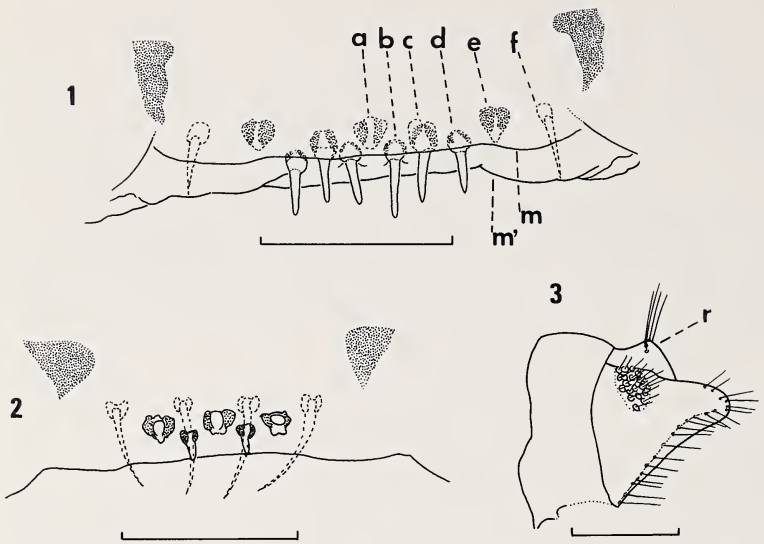
two, is clearly intermediate in two, while two characters remain unknown in this genus.

I conclude on the basis of these comparisons 1) that *Austropsocus* and *Zelandopsocus,* find their closest affinities with the Pseudocaeciliidae and should be placed there; 2) *Bryopsocus* is in several respects intermediate between these two families; it is unusual in several respects (see diagnosis, below) and apparently is best placed in a distinct family; 3) the forms remaining in Philotarsidae are the genera assigned to Subfamily Philotarsinae by Thornton (1981) (Thornton's other Subfamily, Zelandopsocinae, consists of *Zelandopsocus, Austropsocus,* and *Bryopsocus*).

It is necessary, then, to assign the genera placed in Philotarsidae by Thornton (1981) to three families: Philotarsidae Pearman, Bryopsocidae new family, and Pseudocaeciliidae Pearman. The three families may be diagnosed as follows:

Philotarsidae Pearman (type *Psocus picicornis* Fabricius). Most "outer" and all "inner" sensilla of distal margin of labrum occupying a trough in margin, 4 on its outer and 5 on its inner wall; 2 most lateral sensilla on outer surface of labrum (total of 11—"Type 1" of Table 1) (Fig. 1); lacinial tip with lateral tyne relatively broad; tarsi in adult 2- or 3-segmented; pretarsal claws each with a distinct preapical denticle and a slender pulvillus; M-Cu stem in forewing generally with one rank of setae; abdomen lacking eversible vesicles; aedaegus rounded apically; external parameres not protruding much beyond tip of aedeagus; hypandrium lacking paired lateral lobes; subgenital plate one-lobed distally; second valvula bearing a low, rounded lobe medio-distally. Included genera: *Philotarsus* Kolbe, *Aaroniella* Mockford, *Broadheadia* Mockford and Evans (regarded as a synomym of *Aaroniella* by Thornton), *Haplophallus* Thornton, *Tarsophilus* Mockford and Broadhead, *Latrobiella* Thornton.

Bryopsocidae new family (type *Austropsocus townsendi* Smithers). Lacinial tip with lateral tyne somewhat less broad than in Philotarsidae; tarsi in adult 3-segmented; pretarsal claws each with a distinct preapical denticle; M-Cu stem in forewing with two ranks of setae; Cu_2 in forewing with or without setae; hypandrium lacking paired lateral lobes but with a single low, rounded lobe on each side; aedeagus pointed apically; external parameres protruding well beyond tip of aedeagus; subgenital plate one-lobed distally; second



Figs. 1–3. Structures of Philotarsid and Pseudocaeciliid psocids. Figs. 1 and 2. Distal margin of labrum in posterior view showing sensilla (scale = 0.05 mm). Fig. 1. *Latrobiella paraguttata* Thornton and New ♀, type 1: 11 sensilla of three series, a, c, and e lying immediately under a posterior membranous fold (m), b and d lying deeper, perhaps on inner surface of second membranous fold (m'), and f lying on anterior surface. Fig. 2. *Zelandopsocus cumulus* Thornton and New ♀, type 2: nine sensilla in two series, five shown in solid lines on posterior surface, four shown in dashed lines on anterior surface. Fig. 3. *Zelandopsocus cumulus* ♀, clunium, epiproct, and left paraproct in lateral view; r = setigerous ridge or flap of epiproct (scale = 0.2 mm).

valvula bearing a blunt-tipped process medio-distally. Included genus: *Bryopsocus* Thornton, Wong, and Smithers.

Several unusual features were noted for *Bryopsocus* by Thornton, Wong, and Smithers (1977). These include hardening and fusion of female abdominal terga, a setose forewing membrane, and possibly wings of macropterous males being held flat over the abdomen at rest, those of one side overlapping those of the other. These characters, along with the unusual habitat of moss, serve to strengthen the view that this genus should be assigned its own family. The two species which have been assigned to *Bryopsocus* differ rather markedly, and it is not clear that all of the generic characters (derived from the type species) apply to both species.

Pseudocaeciliidae Pearman (type *Psocus citricola* Ashmead). Distal margin of labrum with 4 sensilla on outer wall in form of relatively long, thin-walled setae with acuminate tips and 5 sensilla of usual form in pockets or shallow trough on inner wall ("type 2" of Table 1) (Fig. 2); lacinial tip with lateral tyne relatively slender; tarsi in adult 2- or 3-segmented; pretarsal claws generally lacking preapical denticle, at most with a minute denticle (*Cladioneura,* some *Pseudocaecilius, Mesocaecilius quadrimaculatus* Okamoto); pulvillus broad; M-Cu stem in forewing generally with two ranks of setae; abdomen with one or more ventral eversible vesicles; hypandrium generally with paired lateral lobes or processes; aedeagus pointed apically; external parameres extending well beyond tip of aedeagus; subgenital plate bilobed distally; second valvula bearing an acuminate process medio-distally.

The curious genus *Trimerocaecilius* Meinander was placed here, apparently correctly, by its author (Meinander 1978). It is known to differ from the above description by the following characters: lacinial tip with lateral tyne short and truncate; pretarsal claw with a well formed preapical denticle; pulvillus slender; hypandrium with no trace of lateral lobes or processes. I did not include *Trimerocaecilius* in my Table 1 because information is vague or lacking for it about three of the characters being compared: nature of the apex of the aedeagus, nature of the labral sensilla, and presence or absence of abdominal eversible vesicles.

In addition to the unifying characters noted in Table 1, certain other observations bear on the unification of the 2-tarsal segmented and 3-tarsal segmented forms of this family. The dorsal setose flap noted by Thornton, Wong, and Smithers (1977) of the female epiproct of *Zelandopsocus,* (the "flap" is a rather low ridge in *Z. cumulus,* Fig. 3), which always bears a transverse row of setae, is also present in *Pseudocaecilius, Ophiodopelma,* and *Pseudoscottiella.* The endophallic sclerotizations of some species of *Zelandopsocus,* and *Austropsocus,* are similar to those of some species of *Allocaecilius, Cladioneura, Heterocaecilius, Scytopsocopsis,* and in *Mesocaecilius quadrimaculatus.* Included genera: *Pseudocaecilius* Enderlein, *Allocaecilius* Lee and Thornton, *Allopsocus* Banks, *Austropsocus,* Smithers, *Cladioneura* Enderlein, *Heterocaecilius* Lee and Thornton, *Mesocaecilius* Okamoto, *Ophiodopelma* Enderlein, *Phallocaecilius* Lee and Thornton, *Pseudoscottiella* Badonnel,

Table 1. Distribution of characters in some genera of Philotarsidae and Pseudocaeciliidae.

	# Tarso-meres	Claw w subap. denticle	Hypandrium w paired lat. lobes/ processes	Aedeagus pointed (rounded) apically	Ext. parameres reach far beyond aedeagus
Philotarsus	3	+	−	Rounded	−
Haplophallus	3	+	−	Rounded	−
Aaroniella	3	+	−	Rounded	−
Latrobiella	3	+	−	Rounded	−
Tarsophilus	2	+	−	Rounded	−
Bryopsocus	3	+	−	Pointed	+
Zelandopsocus	3	−	+	Pointed	+
Austropsocus	3	−	+	Pointed	+
Pseudocaecilius	2	− (some +)*	±	Pointed	+
Mesocaecilius	2	− (some +)*	+	Pointed	+
Ophiodopelma	2	−	+	Pointed	+
Scytopsocus	2	−	+	Pointed	+

*In some species of *Pseudocaecilius*, and in *Mesocaecilius quadripunctatus*, there is a minute denticle on one claw per tarsus.

Subgen. plate 1/2 lobed distally	Labral sensilla: type 1 or 2	Lacinial tip. lat. tyne	Setae on M-Cu stem in FW: 1 or 2 ranks	Appendage of 2nd valvula rounded/ptd.	Abdom. eversible vesicles
1	1	Broad	1	Rounded	–
1	1	Broad	1	Rounded	–
1	1	Broad	1	Rounded	–
1	1	Broad	1 or 2	Rounded	–
?	1	Broad	1	?	–
1	?	Inter.	1	Blunt Point	?
2	2	Inter. or narrow	1	Pointed	+
2	2	Narrow	2	Pointed	+
2	2	Narrow	2	Absent	+
2	2	Narrow	2	Pointed	+
2	2	Narrow	2	Pointed	+
2	2	Narrow	2	Pointed	+

Scottiella Enderlein, *Scytopsocopsis* Lee and Thornton, *Scytopsocus* Roesler, *Trichocaecilius* Badonnel, *Trimerocaecilius* Meinander, *Zelandopsocus* Tillyard.

It is likely that the adaptive zones of the three families are generally distinct. The combination of absence of (or only minute) preapical denticles on the pretarsal claws, possession of broad pulvilli, and presence of ventral abdominal eversible vesicles in most Pseudocaeciliidae probably signifies leaf dwelling, which is known for several of the genera. Presence of preapical denticles of the pretarsal claws, slender pulvilli, and absence of abdominal eversible vesicles in Philotarsidae may signify bark dwelling, as is the case in the *Philotarsus* and *Aaroniella* species which I have observed. Some of these characters remain unrecorded for Bryopsocidae. The type species of this family has been taken most frequently on moss, suggesting a unique habitat for this group.

The correlation of some of the characters to habitat noted in the above paragraph suggests the possibility of convergence between three-tarsal-segmented forms (Philotarsidae *sensu* Thornton, 1981) and two-tarsal-segmented forms (Pseudocaeciliidae *sensu* Lee and Thornton, 1967), but the hypothesis of phylogenetic affinity proposed here appears to be the simpler one and is supported by several characters which are not habitat-correlated.

Can a sister-group relationship be seen among these families? In dealing with this question, one must note that Smithers (1967) presented a very strong argument for close proximity of Family Pseudocaeciliidae and Family Calopsocidae. This idea is not at all weakened by addition of *Austropsocus* and *Zelandopsocus* to Pseudocaeciliidae. Unless Calopsocidae, in which forewing venation has become complex and plastic, was derived from within the venationally conservative Pseudocaeciliidae, these two families must have phylogenetic sister relationship.

Judging from the extent of character sharing shown in Table 1, Bryopsocidae is probably the phylogenetic sister group of the common stem of Pseudocaeciliidae and Calopsocidae. However, certain intriguing similarities occur in the wing, tarsal, and female genitalic characters of Calopsocidae and Archipsocidae which require further exploration. Secondary suppression of some of the Pseudocaeciliid characters may also have produced Family Trichopsocidae.

The Philotarsidae as defined here may be the sister group of the common stem of Bryopsocidae plus the Pseudocaeciliid-Calopsocid branch, but not necessarily. An argument of about equal strength could be made for a liaison between Philotarsidae and Mesopsocidae or Philotarsidae and Elipsocidae. I do not believe that present data are sufficient to solve this problem.

Summary

A comparison of genera of Families Philotarsidae and Pseudocaeciliidae indicates that the classification of Family Philotarsidae proposed by Thornton (1981) is unacceptable. The two major genera of his subfamily Zelandopsocinae (*Zelandopsocus* Tillyard and *Austropsocus* Smithers) are more closely related to Family Pseudocaeciliidae than to his other subfamily, Philotarsinae. One new family, Bryopsocidae, is erected for *Bryopsocus* Thornton, Wong, and Smithers. This genus is intermediate in several respects between Philotarsidae and Pseudocaeciliidae (both families as redefined here) and is unique in several others. Families Philotarsidae and Pseudocaeciliidae are redefined and the named genera assigned to each are listed. *Zelandopsocus* and *Austropsocus* are transferred from Philotarsidae to Pseudocaeciliidae. Pseudocaeciliidae and Calopsocidae appear to be sister groups. Bryopsocidae may be a sister group to this pair, but certain alternatives are possible. Philotarsidae may be a sister group to the trio Pseudocaeciliidae-Calopsocidae-Bryopsocidae, but several other families, including Archipsocidae, Trichopsocidae, Elipsocidae, and possibly Mesopsocidae would have to be investigated for a complete understanding of the Phylogeny of these groups.

Acknowledgments

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BEHAVIORAL FLEXIBILITY OF TEMPORAL SUBCASTES IN THE FIRE ANT, *SOLENOPSIS INVICTA* IN RESPONSE TO FOOD

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Introduction

Most social insects are characterized by the presence of a caste system (Oster and Wilson 1978). Castes are functionally defined as any set of colony members, smaller than the society itself, that specialize on particular tasks for prolonged periods of time (Michener 1974; Oster and Wilson 1978). The performance of these tasks may be correlated with size (physical castes) or age (temporal castes) of the worker. As a rule, workers in physical castes cannot shift easily from one role to another. They tend to specialize in certain tasks predetermined by their brain structure, sensory physiology, and innate behavior patterns (Oster and Wilson 1978). In contrast, workers in temporal castes usually follow an age-related progression from nurse duties to nest duties to foraging. Studies on temporal castes in honeybees (Nolan 1924; Rösch 1930) and ants (Ehrhardt 1931; Dobrzańska 1959; Chavin 1969; Lenoir 1979) showed that this progression is not necessarily rigid. Workers can respond to colony needs by altering either the rate or the direction of a typical behavioral sequence. In the present study, we examined the behavioral flexibility of the temporal caste system of the fire ant, *Solenopsis invicta* Buren.

Fire ant workers are weakly polymorphic and show slight allometry with continuous size variation and three arbitrarily demarcated size categories of workers in mature colonies (Wilson 1953; 1978). Superimposed on these morphological castes is a temporal division of labor which largely determines which tasks will be performed

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(Mirenda and Vinson 1981). There are two behaviorally discrete subcastes, nurses and foragers, and a third intermediate subcaste, reserves, that are transitional in behavior. Workers typically progress from nursing to nest maintenance to foraging. However, they progress at different rates depending on size which, in turn, is correlated with longevity.

To access the flexibility of the temporal caste system, we focused on tasks that were critical to the survival of the colony: the maintenance of an adequate food supply to the queen and brood. The use of radioiodinated protein and differentially marked subcastes enabled us to trace resource flow through the colony. Normally, foragers exclusively forage, nurses exclusively tend brood, and reserves mainly relay food from foragers to nurses (Mirenda and Vinson 1981; Sorensen et al. 1981). By selectively eliminating temporal subcastes we were able to assess the ability of the remaining subcastes or subcaste to alter their current response behavior to food and replace the missing workers.

Materials and Methods

Ants used in these experiments were from polygynous colonies collected in College Station, Texas. Laboratory maintenance procedures were as described previously (Sorensen and Vinson, 1981). To separate temporal subcastes, colonies were transferred to behavioral distribution nests (Sorensen et al. 1981) and separated by their location inside and outside the nest during food presentation. Subcaste members were then chosen at random and marked with fine colored wires (Mirenda and Vinson 1979). They were placed in two stacked clear plastic cylinders (7 cm high, 10 cm diam., Sorensen and Vinson 1981) with the upper chamber as a foraging area and the lower chamber containing a small shell vial to serve as a brood chamber. Brood and queens from the mother colony were added and held with the workers for 24 h. Radioiodinated albumin mixed with egg yolk powder (Sorensen and Vinson 1981) was then placed in the upper foraging chamber and replenished as needed over 7 days. Radioactivity was measured with a Searle 1195 gamma radiation counter. Workers were measured daily in gelatin capsules and returned to their respective containers (Sorensen et al. 1980). Larvae were measured together in one capsule to minimize handling.

Members of the three temporal subcastes were tested by themselves (i.e., two subcastes excluded) and in paired combinations to determine if adequate food flow could be maintained. Three replications. of the following groups were tested using a different colony (A, B, and C) each time. With two of the three subcastes excluded, we tested 50 foragers (F), 50 larvae (L), and 1 queen (Q); 50 reserves (R), 50 L, and 1 Q; and 50 nurses (N), 50 L, and 1 Q. With one subcaste excluded we tested combinations of 25 F/25 N, 50 L, 1 Q; 25 F/25 R, 50 L, 1 Q; and 25 R/25 N, 50 L, 1 Q. Five replications using workers from all three subcastes were tested as a control using 18 F/18 R/18 N, 50 L, and 1 Q. Different colonies from those previously tested were used.

To determine the biological half-life of the radiolabelled protein in the different groups tested (Sorensen et al. 1980) control colonies were set up as described previously, allowed to feed for 1 h, and held for 7 days without food. All of the ants were measured daily for radioactivity as described previously.

Statistical analyses were done using the Statistical Analysis System (SAS) for computer data analysis. We used a SAS REG procedure for full rank linear model analysis, regressing the amount of food in each ant against the total amount of food in the colony. Multiple comparisons among slopes were made using the Newman-Keul Multiple Range Test (Zar 1974). Duncan's Multiple Range Test for means (SAS GLM procedure) was used to compare the mean amount of food collected by test colonies over time.

Behavioral observations were made on marked foragers and nurses to determine how flexible these subcastes were with regards to foraging and brood tending behavior. We isolated 100 nurses with larvae, marked them with wires, placed them in stacked cylinder nests as previously described, and presented them with food twice daily. Nurses that entered the foraging chamber were marked with a second wire loop. We then added 100 marked foragers and 100 reserves and observed them during feeding to see if the doubly marked N/F continued to forage or returned to brood tending. Three different colonies were tested. Foragers were tested in a similar manner except that foragers that stayed in the brood chamber were differentially marked and then later observed in the reconstituted colonies to see if they remained with the brood or returned to the nest periphery or foraging chamber.

Results

The biological half life of ^{125}I-albumin in workers, queens, and larvae is shown in Fig. 1. Without any additional labeled food entering the colony, the level of radioactivity in queens and larvae dropped below 50% by the third day and remained at 40% and 11%, respectively. The level of radioactivity in the workers stabilized at 65–70% after four days. This pattern was seen in all of the treatments, regardless of which subcastes were present. By superimposing this background pattern on those obtained when labeled food was allowed to enter the colony freely, we were able to estimate the amount of additional food distributed.

The relationship between total amount of food collected per colony and the partitioning of that food among subcaste members is illustrated in Figure 2. The daily amount of food collected per ant was regressed against the daily total of food collected by the colony. As the quantity of proteinaceous food in the colony increased, the rate at which the queen accumulated food was significantly higher than that of the larvae, reserves, nurses, and foragers. The rates at which larvae and reserves received food were significantly higher than that of the nurses and foragers.

A summary of the mean amount of food brought in by each colony over a one week period is shown in Figure 3. Three different colonies (A, B, and C) were used in the treatment groups and five other colonies used in the control groups. There were significant differences in the quantity of food collected by foragers, nurses, or reserves held by themselves. With nurses, a time delay of 3 days occurred before foraging was initiated. Paired worker subcastes also showed some variability in foraging activity. Overall, groups of foragers alone collected significantly more food than groups without foragers present with the exception of one R/N trial. The food collected by a mixture of all 3 subcastes was similar to that collected by R/N combinations or groups of nurses or reserves by themselves. There was, however, considerable variation in mean protein collected. Ants from colony C collected more food than ants from either colony A or B in most cases and ants from colony B collected less food in most cases.

Table 1 presents a summary of least square means (ug protein/ant) using the total food per colony as a covariate. This minimizes the effect that quantity of food in the colony has on the food

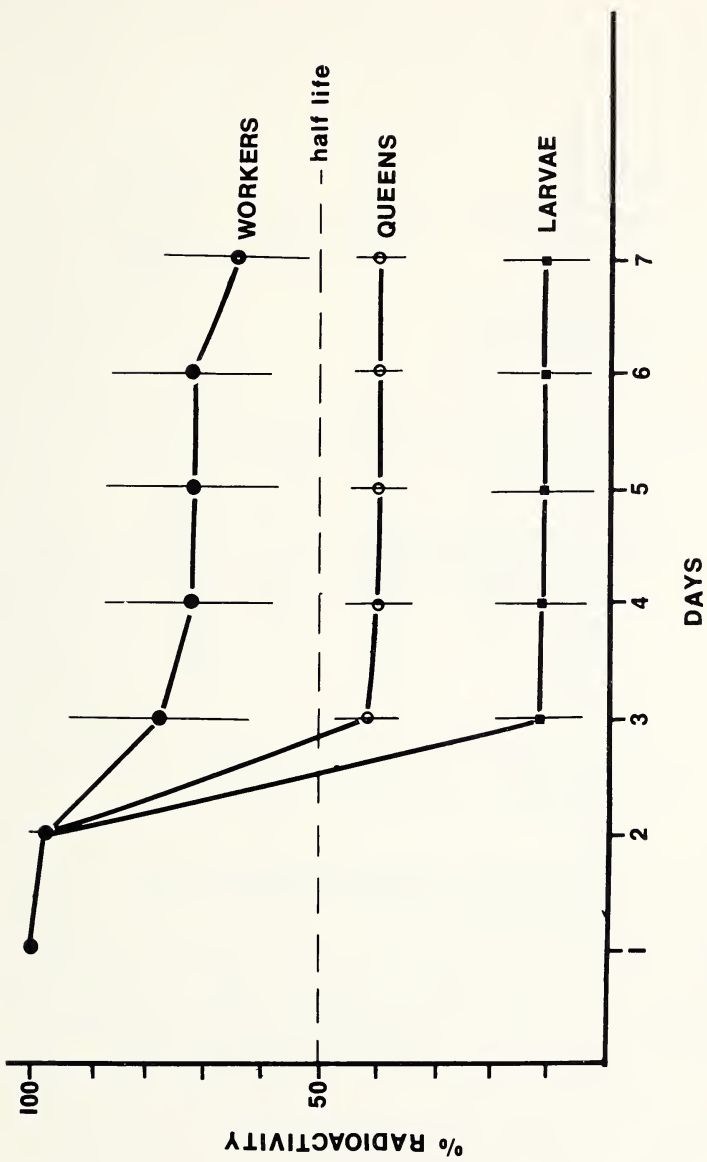

Fig. 1. The biological half life of ^{125}I-albumin in workers, queens, and larvae. All subcaste combinations were tested and held seven days without food after their initial feeding of labeled food. Standard deviations are shown.

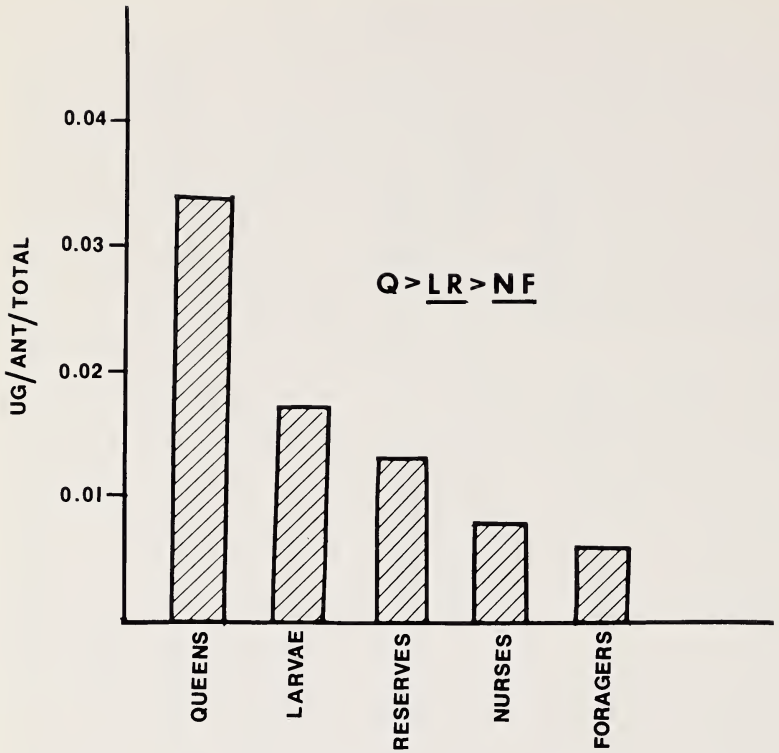

Fig. 2. The quantity of egg yolk per subcaste member is shown as a function of the amount of egg yolk in the colony. Underlined groups do not differ significantly at the $p = 0.05$ level using the Newman-Keul Multiple Range Test.

collected per subcaste and enables us to compare feeding efficiency as if all of the colonies had collected the same amount of food. Larvae held with nurses or reserves received significantly more food than larvae tended by foragers alone. Larvae held with nurses and either reserves or foragers received significantly more food than larvae tended by foragers and reserves. Larvae in F/N/R combinations received as much or more food than larvae tended by other subcaste combinations. Queens received significantly more food when tended by foragers alone than by either reserves or nurses. F/N groups fed their queens significantly more food than either the R/N or F/R worker combinations. Overall, queens tended by foragers or foragers and nurses received significantly more food

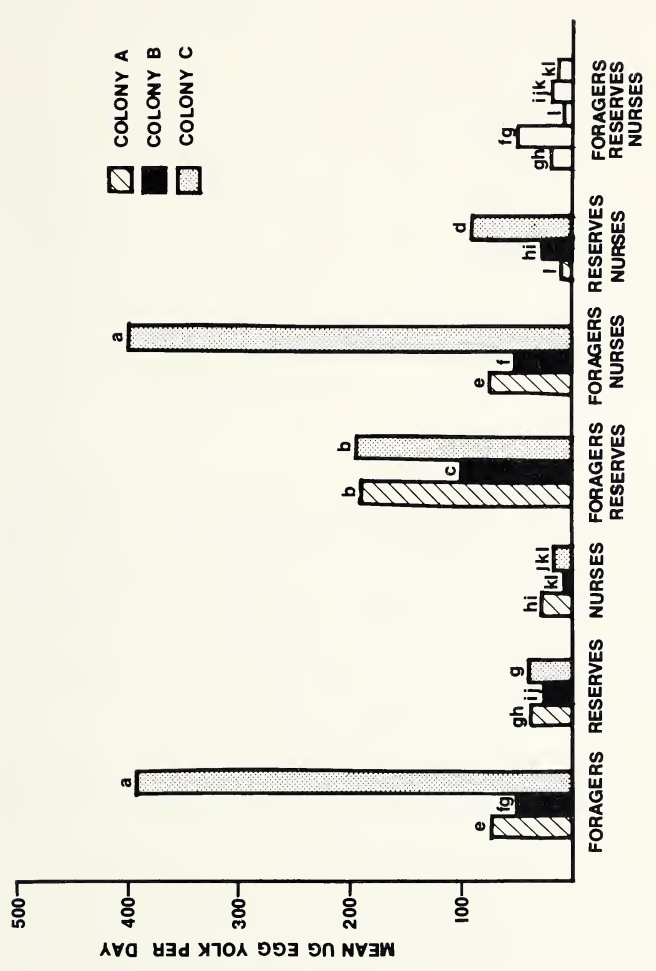

Fig. 3. The mean amount of egg yolk taken daily by the subcaste members is shown for each treatment combination. Three colonies (A, B, and C) were used for the majority of treatments as shown. The same letter above two or more bars indicates that these means are not significantly different at the 0.05 probability level using Duncan's Multiple Range Test.

Table 1. Mean amount of food (ug) contained by foragers (F), reserves (R), nurses (N), queens, and larvae in various tretment combinations. Least square means and standard error in parentheses are given using the amount of food per colony as a covariate.

Subcaste	F/R[1]	F/N	R/N	F	N	R	F/N/R
Foragers	2.8a	2.0b	---	2.5a	---	---	1.5b
	(0.8)	(0.3)		(0.3)			(0.3)
Reserves	2.3a	---	0.9b	---	---	1.1b	0.8b
	(0.2)		(0.2)			(0.2)	(0.1)
Nurses	---	0.9a	0.9a	---	0.6b	---	0.7b
		(0.1)	(0.1)		(0.1)		(0.1)
Queens	2.0b	5.3a	0.8b	6.1a	0.8b	1.5b	4.4b
	(1.2)	(1.2)	(1.2)	(1.2)	(1.6)	(1.2)	(0.8)
Larvae	17.9c	39.9ab	42.3ab	32.1b	42.1ab	35.6ab	43.8a
	(4.3)	(4.4)	(4.2)	(4.3)	(5.2)	(4.3)	(2.9)

a. Least square means followed by different letters are significantly different at $p < 0.05$ for each subcaste group. Larvae were measured together, 50 larvae per measurement.

than queens tended by other worker groups. Foragers paired with reserves or by themselves accumulated significantly more food than foragers paired with nurses or with nurses and reserves. Nurses received significantly more food when paired with either foragers or reserves than when paired with both foragers and reserves or left alone as a group. Reserves accumulated significantly more food when paired with foragers than when by themselves, paired with nurses, or held with both nurses and foragers.

When we observed marked nurses, we again saw a 3 day delay before any nurses entered the foraging chamber and only 10% of the nurses were foraging after one week (data not shown). When reserves and foragers were added, none of the marked nurse/foragers returned to the brood chamber but remained on the nest periphery and at least 50% of them actively foraged for food. When isolated with brood, 50–60% of the foragers remained with the larvae and did not forage (data not shown). When nurses and reserves were added, only 5–10% of these marked forager/nurses remained with the brood, 70% returned to the nest periphery, and 20% actively foraged for food.

Discussion

Colony fitness in *S. invicta* is maintained by an efficient system of resource provisioning which is responsive both to the nutritional requirements and degree of hunger of its members and to how much food is available (Howard and Tschinkel 1981; Sorensen and Vinson 1981; Sorensen et al. 1983). In the present study, we utilized this system of resource provisioning to examine whether or not temporal subcaste members could change their roles of either feeding larvae (nurses), relaying food (reserves), or foraging (foragers) when other subcastes were removed.

We found that queens were fed protein preferentially regardless of amount available, presumably assuring their current and future reproductive output. Larvae were also fed protein preferentially as it entered the colony. The same partitioning of protein in response to supply was seen even after the experimental elimination of two of the three worker subcastes. This indicated that the behavior of workers was flexible enough to allow the colony to maintain priorities of resource provisioning even during severe disruption.

Foraging activity was greater in groups of foragers than in reserves or nurses and when they were present, significantly more food entered the colony than when they were absent. Similarly, nurses were slightly more active than reserves at feeding larvae and significantly more active than foragers. Reserves were intermediate between foragers and nurses in their ability to forage and feed larvae, performing the latter task more actively. Differences among colonies in feeding activity on egg yolk were reflected in similar differences among the subcastes isolated from those colonies. Differences in feeding preferences of fire ant colonies have been documented by Glunn et al. (1981) for both laboratory and field colonies.

Assessing the degree to which workers could switch to a different behavior, we found that reserves and nurses were considerably less active than foragers at food gathering. When nurses were grouped by themselves, they did not leave the brood chamber for 3 days and then only a few nurses ventured into the foraging chamber. The few foraging workers which appeared were probably mature nurses making the transition to reserve since marked nurse-foragers did not return to brood tending once colonies were reconstituted. However,

this temporal behavior sequence may have been slightly accelerated by the absence of food as seen in *Bombus sylvarum* and other *Bombus* species (Free 1955). Acceleration of the development of behavior of younger workers in the absence of older workers has also been reported for the ant species *Manica rubida* (Ehrhardt 1931), *Formica sanguinea* (Dobrzanska 1959), *Formica polyctena* (Chauvin 1969), and *Tapinoma erraticum* (Lenoir 1977). These researchers found that groups of young workers of the same age quickly organize themselves into nurses and foragers. Lenoir (1979) found that this behavior was sometimes reversible and after a few days, young workers ceased foraging and became nurses again. In fire ants, however, nurses did not appear to be as flexible and did not resume active brood tending after foraging.

Reserves continued to tend brood when isolated as a group but also showed a limited tendency to forage. No delay in switching to foraging was evident. While reserves can be recruited by foragers for food collection (Sorensen et al. 1981), they normally do not leave the nest to forage on their own initiative (Mirenda and Vinson 1981). Similar differeneces in the capabilities of young and middle-aged workers to shift to the roles of the oldest workers are seen in *Pheidole dentata* (Oster and Wilson 1978).

Isolated groups of foragers did feed and tend larvae in addition to foraging but remained primarily on the nest periphery when inactive rather than in the brood chamber where nurses or reserves were commonly found. Role flexibility in foragers with respect to brood tending has been seen in both *Myrmica rubra* (Ehrhardt 1931) and *M. ruginodis* (Weir 1958a, b). The immediate switch that we saw for both foragers and reserves to tending larvae when isolated with them argues against exocrine gland control of behavior as seen in *M. rubra* (Cammaerts-Tricot 1974) or *B. hyphorum* and *B. terrestris* (Röseler 1967).A delay in response would be expected if dormant exocrine glands had to be reactivated (Oster and Wilson 1978). Location in the nest may have been more important in determining probability of worker response. Seeley (1982) found that tasks performed by honeybees are strongly influenced by nest architecture. In the present study, proximity to larvae alone appeared to induce brood tending behavior by workers. The majority of foragers returned to foraging when nurses and reserves were added to their colonies.

The queen continued to receive food regardless of which subcaste members were present, indicating that all workers were responsive to her needs. However, queens received more food from foragers than from nurses or reserves. This may have been related to the tendency of older ants to regurgitate food more readily than younger ants (Mirenda and Vinson 1981). It may also have been due to the presence of more food, increasing the probability that the queen would be fed (Howard and Tschinkel 1981). We do not know which subcaste members feed the queen in field colonies. Access to the queen, normally sequestered near the brood, may be limited to nurses and reserves. However, Brian and Jones (1980), in their studies with *M. rubra,* found that foragers associate with and pass food directly to the queen. They also cite similar findings for *Oecophylla longinoda* and *Lasius niger.* They feel that it may be a general phenomenon in all ants that foragers are more queen oriented and thus more susceptible to her influence over behavior than nurses.

In summary, these experiments indicated that the normal sequence of response behavior to food in fire ant workers could be altered. This ability of workers to switch to a new behavioral role in response to colony needs insures a steady flow of food to the queens and larvae. For fire ants, behavioral flexibility of workers greatly increases the chances of colony survival.

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THE IDENTITY OF *HADENA HAUSTA* GROTE (NOCTUIDAE, LEPIDOPTERA)*

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Hadena hausta Grote 1882 was described from a single male from Kittery Point, Maine. Since that time this taxon has been largely ignored. Hampson (1908) sank *H. hausta* as a synonym of *Miana semicana* Walker, 1865. McDunnough (1938) and Forbes (1954) followed this placement. Franclemont and Todd (1983) listed both of these taxa as separate species, but their checklist format does not indicate the basis for this decision. Hampson and all of these subsequent authors placed both taxa in *Oligia.* Since Hampson based his interpretation of *H. semicana* on the type, I accept it as correct. Also, he illustrates this taxon (Plate CXVIII, fig. 3) and his figure seems to match the description of *Oligia semicana* given by Forbes (1954).

While I was curating the Noctuidae in the collection of the Museum of Comparative Zoology, I located a specimen labelled as the type of *Hadena hausta,* (M.C.Z. type 1838) along with an accompanying genitalia slide (#M.C.Z. 477). This specimen (Fig. 1) agrees with the original description and the collection data given in the description match those on the specimen. Thus this appears to be an authentic Holotype. It is not conspecific with the specimen figured by Hampson.

O. hausta is somewhat browner than *O. semicana* and differs in having a prominent black dash or wedge in the fold of the forewing much like that present on *O. exhausta* (J. B. Smith), but thicker and less sharply defined. Hampson's figure also seems to indicate a distinctly whitish antemedian line on *O. semicana.* This line has at most some white in its posterior half on *O. hausta* and it is much more evenly curved on the latter species. From *O. exhausta, O. hausta* can be separated by its browner color and whiter reniform,

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Fig. 1. Holotype of *Hadena hausta* Grote. Actual length of primary is 10.6 mm.

perhaps most reliably by the lack of an anal dash beyond the postmedian line, and by the fact that the space between the reniform and the postmedian line is at least partially of the pale color that dominates the subterminal space. The space between the reniform and postmedian line is concolorous with the rest of the median area on *O. exhausta*. *O. crytora* (Franclemont), *O. tonsa* (Grote) and *O. semicana* agree with *O. hausta* on this character. The posterior end of the reniform touches the postmedian line on all four *O. hausta* before me, but this is the case on only five of 35 *O. exhausta* examined.

Oligia hausta is apparently rare in collections. The fact that Forbes did not regard it as distinct suggests that he was not familiar with it. Besides the type, which is dated 11 July 1882, there are two other specimens in the MCZ collection from Peggy's Cove and Digby, Halifax Co., Nova Scotia, 11 and 14 July 1953, *leg.* D. C. Ferguson. I have another on loan from Scott Smedley who collected it at the Wellfleet Bay Audubon Sanctuary on Cape Cod, Massachusetts, 18–19 June 1983 in a mosaic of salt and freshwater wetlands. He reports taking another on 22–24 June. These will be

deposited in the Cape Cod Museum of Natural History, in Brewster. All specimens seen are males.

Mark Mello has a specimen of one of the two taxa that commonly pass for *O. semicana* in New England from the Wellfleet site. It differs from Hampson's figure in that there is no prominent antemedian line and the entire forewing inside the postmedian line is rather uniform dark gray, except for the paler reniform.

The differences in maculation of the forewing between *O. hausta* and the other species in the *exhausta-semicana* section of *Oligia* seem sufficient to justify treating *O. hausta* as a valid species as was done by Franclemont and Todd. This species seems to combine characters of the immediate *semicana* group and the distinctive *O. exhausta.*

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